

**THE PARASITOID COMPLEX OF *EUXOA OCHROGASTER* (GUENÉE)
(LEPIDOPTERA: NOCTUIDAE)**

A. C. SCHAAF

Sugar Research Department
Sugar Manufacturers' Association
Mandeville P. O., Jamaica, W. I.

Quaestiones entomologicae
8 : 81-120 1972

Twenty-seven species of parasitoids have been recorded as being reared from Euxoa ochrogaster (Guenée). Three of these records are not valid because they are based on mis-identifications. Descriptions of the available immature stages of 15 species are provided. Of the remaining species, four had been previously described, two could not be studied because of taxonomic difficulties, and no material was available of three more. A brief discussion of the host specificity and the role of the parasitoids in regulating E. ochrogaster populations is given.

Vingt-sept espèces de parasitoids ont été spécifiées comme faisant partie de l'Euxoa ochrogaster (Guenée). Cependant, trois de ces spécifications se sont relevées fausses à cause de certaines erreurs d'identification. Des descriptions de 15 espèces à l'état précoce sont publiées. Concernant le reste, quatre ont été antérieurement décrites, deux de ces espèces n'ont pas pu être observées encore de façon spécifique à cause de difficultés d'ordre taxonomique et les trois autres demeurent inconnues par manque de matériels. Une brève discussion sur la spécificité et le rôle des parasitoids en relation avec le contrôle des groupes d'E. ochrogaster a été pourvue.

The red-backed cutworm, *Euxoa ochrogaster* (Guenée) is a well-known, destructive ground cutworm native to the prairie provinces of Canada. The purpose of this study is to provide a method of identifying some of the immature stages of the parasitoids of the red-backed cutworm. Some groups of parasitoids are difficult to identify to species as adults but may be identified using morphological or behavioural characters of immature stages. The advantages of recognizing the immature stages of the parasitoids of any host species are: 1. If research with live adult parasitoids is necessary, identification using the remains of the immature stages prevents damage to the living specimens. 2. It is not necessary to rear either the host or the parasitoids to maturity to obtain data on the host-parasitoid relations. This allows analysis of host specimens which died, and of hosts killed to enlarge a sample size when there was no time to rear all the hosts or parasitoids to maturity. 3. Super-, hyper-, or multiple parasitoid attack can usually be recognized only by the dissection of host material before any of the parasitoids can mature and emerge. Analysis of inter-specific and intra-specific competition of parasitoids as well as the interactions with predators and disease is possible from the results of such dissections.

The term parasitoid is used in this paper rather than parasite which is usually used when referring to entomophagous groups which attack single host units. The need for the term parasitoid arises from the fact that ecologically the action of such entomophagous species is different from that of either predators or true parasites. Doutt (1964) outlined the ways in which parasitoids differ from parasites.

PROCEDURES AND REVIEW

Materials and methods

This research was started during the summer of 1967 in conjunction with the work of Dr. J. H. Frank (1971a, b) on the predator complex attacking *E. ochrogaster*. The field research was carried out at Calahoo, Alberta on the farm of Mr. C. Bergstreiser. The location

of the field site was South-west 8, Township 55 — Range 27: West 4th Meridian. This site was first investigated June 22, 1967 following a report of a cutworm outbreak to the Alberta Department of Agriculture. The outbreak was limited in both cutworm numbers and in area attacked and little damage was caused. Most of the cutworms were in the final instar. The center of the outbreak was used as a test area and the balance of the field was sprayed with insecticide. During the spring and summer of 1968, plots were established in an oat field adjacent to the barley field in which the outbreak had occurred the year before. The oat field was summer-fallowed the year before. Cutworms were collected in two types of pitfall traps: 3.05 m x 0.12 m eavestroughs and plastic containers 8.7 cm diameter at the top x 10.2 cm depth, by hand collecting, and by systematic sieving of quadrat samples. The numbers of cutworms captured were higher than the season before but inadequate for a meaningful population study of either the host or its parasitoids. All live hosts were reared in both 1967 and 1968. A small number of cutworms was collected in 1969 at Calahoo using 3.05 m eavestroughs as pitfall traps and preserved for further study.

Captured cutworms were reared in the laboratory in individual plastic petri dishes. Each dish was provided with moist filter paper and fresh dandelion (*Taraxacum officinale* Weber) leaves on at least every second day. The dishes were changed when feces had badly contaminated the filter paper. To prevent or reduce the spread of disease in the laboratory new dishes were used as much as possible or the old dishes were sterilized with a KOH solution. Forceps used to handle specimens were rinsed in 95% ethyl alcohol after each specimen was handled. Dishes infested with mites were changed but mites were still a serious source of mortality in laboratory reared cutworms. Specimens were reared in a controlled temperature cabinet at between 18 and 21 C. All specimens which were found dead in the field (usually drowned) and most of those which died in the laboratory were preserved in 70% ethyl alcohol. Some of the hosts which showed obvious stages of parasitoid attack were killed and stored in alcohol for further study. All hosts which failed to produce either adults or parasitoids were checked by dissection for evidence of parasitoid attack.

The basic parasitoid list was formed using three sources of information. A literature review was carried out to establish all the recorded parasitoids. The best sources of information were King and Atkinson (1928), Thompson (1945), and Graham (1965). Specimens of adult parasitoids which had been reared in my study were compared with known specimens or were identified by Dr. Mason or Dr. Peck of the Entomology Research Institute, Ottawa. The final source of information was host labels on reared specimens in the Canadian National Collection (C.N.C.). The host labels aided by allowing me to find specimens which had originally been recorded at the generic level only, or which were not previously recorded at all.

Specimens of most of the species studied were borrowed from the C.N.C. The only bombyliid personally examined was *Poecilanthrax alcyon* (Say). The only other parasitoid species which I did not borrow specimens of was *Copidodoma bakeri* (Howard).

The methods of differentiating species and the preparation of the specimens for study will be discussed in the sections dealing with each family of parasitoids.

Biology of *E. ochrogaster*

The biology of the red-backed cutworm has been discussed by King (1926), McMillan (1930), and Strickland (1923). Jacobson (1970) gives details of the laboratory ecology. Hardwick (1965) reviews the taxonomy and the geographical range of *E. ochrogaster*.

One useful character is the appearance of the pupa before and after the parasitoids emerge. Fig. 60 shows a typical pupa which would produce an *E. ochrogaster* adult. Directly after the prepupa has molted to the pupa, the cuticle is a pale off-white. The cuticle darkens

quickly to a light brown and remains this color. As the normal pupa develops, it gradually darkens and shortens until just before emergence, when it is very black and the surface is distorted. The adult emerges through the dorsal side and many of the sutures release, leaving the pupal remains badly damaged. The abdominal segments of the pupa are often telescoped anteriorly at emergence (Fig. 61). After emergence, the pupa returns to a light brown color.

Predators, diseases, and non-insect parasitoids

King and Atkinson (1928) list several predators of *E. ochrogaster* immature stages. Frank (1971a) studied the carabid predators of *E. ochrogaster* extensively. I found that the lycosid spider, *Trichosa terricola* Thorell, killed many cutworms in pitfall traps. From its ability to kill even the largest cutworms, it is probably an important predator at Calahoo.

The role of diseases in the control of the red-backed cutworm is in need of study. King and Atkinson (1928) carried out a preliminary study but did not have the pathogen identified. I also found extensive mortality from an unidentified disease in my laboratory colonies.

The only non-insect parasitoid found attacking the red-backed cutworm was a single nematode. It was reared from a fifth instar red-backed cutworm in late June, 1969 from material collected at Calahoo. This specimen was examined by Dr. H. E. Welch, who stated that it probably belongs to the genus *Agamermis* Cobb, Steiner, and Cristie. Positive identification was not possible because the specimen was immature.

TACHINIDAE

The morphology of immature tachinids

The morphology of the final instar larvae and puparia of tachinids, as well as of other higher Diptera, is poorly understood. A recent work by Menees (1962) offers an explanation of the origins of the cephalopharyngeal structures of the various larval instars. In his work he shows that the mouth hooks are chiefly maxillary in origin, and that beyond the first instar there is no evidence of vestigial mandibular structures. Various authors describing these structures use different terminologies which assume different origins of the structures (Zuska, 1963; Sanjean, 1957). Others based their terminologies on convenient names (Finlayson, 1960). The system which I use is outlined in Fig. 1-4 and includes arbitrary terms not based on any morphological assumptions.

The final instar tachinid larva has 12 segments, but the puparium has only 11 due to the invagination of the pseudocephalon and part of the first thoracic segment when the larval skin becomes the puparium (Zuska, 1963). This leaves the cephalopharyngeal structures lying in the immediate anterior end of the puparium, attached to part of the unsclerotized final instar larval skin. Horizontal and vertical sutures in the puparium release when the adult emerges. The flaps which are formed at emergence are connected at their midpoints to the rest of the puparium. The dorsal flap, carrying the anterior spiracles, often is lost. The ventral flap is less often lost and contains the cephalopharyngeal structures.

The puparium retains many of the characters of the final instar larva. One of these characters is the pattern of spinules. Zuska (1963) states that these patterns may vary due to different hosts and other factors, and that thus is not a good taxonomic character. Colour is often used as a character in the description of the puparium (Greene, 1921; Strickland, 1923), but as pointed out by Zuska (1963) and from my observation, the variation is too great for it to be of much use. The most reliable puparium characters to work with are the posterior spiracles (Fig. 3). Unfortunately, the difference between closely related species is not always sufficient. While all of the species in this study had three orificia, some groups

of tachinids have four or more. The cicatrix, remnants of the second instar spiracle, was evident in all specimens studied. As the anterior spiracles are often lost, they are not a good character to base general classifications on. In addition, the number of openings or pori varies intraspecifically.

The cephalopharyngeal structures (Fig. 2) found inside the puparium are generally good characters, but the variability of some of the parts must be considered. Basically, the cephalopharyngeal structures are formed of three sclerites: the anterior, median, and posterior. These may be fused to their adjacent members so that only one or two sclerites are apparent and functional. The anterior parts appear to be very constant whereas the posterior portion may vary a great deal in shape or degree of sclerotization. As the posterior sclerite is the least sclerotized portion of the structure, it may be twisted or bent in such a way as to obscure its true appearance.

Sclerites in addition to the basic three, occur in some species. Sanjean (1957) offers names for three such sclerites in sarcophagid larvae, but there is no evidence to show which are present in my specimens. As the true origin of these sclerites is not known, I have called them auxiliary sclerites. While dissecting the host, the cast cephalopharyngeal structures of earlier instars may be found but not often enough to be of use in identifying a species.

Gonia Meigen

The concept of the genus *Gonia* has been reviewed by Tothill (1924), Morrison (1940), and Brooks (1943). Brooks regarded *Gonia* as a composite of several genera which he separated and described. His work separated the species which I am considering into three genera: *Gonia* (*capitata*, *sequax*); *Reaumuria* (*aldrichi*), and *Fuscigonia* (*fuscicollis*). Sabrosky and Arnaud (1965) restored *Gonia* to its original concept, which will be used in this paper. As will be shown in the discussion of the species of this genus, more work is needed on their taxonomy.

The characteristics of *Gonia* puparia are as follows. The puparia are robust, larger than 9 mm in length, and are patterned or completely covered with spinules. The posterior spiracles are large, protruding, and heavily sclerotized while the anterior spiracles are diverse in character. The anal protuberance is small and insignificant. The cephalopharyngeal structure is two-articled with the anterior and median sclerites being fused. The dorsal anterior portion of the posterior sclerite forms an arm which projects forward to the anterior sclerite. A sclerotized band of different widths surrounds the inner angle between the dorsal and ventral processes of the posterior sclerite. The entire structure of the cephalopharyngeal apparatus has a triangular form with the lines of the anterior-median and posterior sclerites being nearly straight.

The females of this genus typically lay their eggs on vegetation which may be eaten by host larvae. The eggs hatch in the host gut and the larvae penetrate into the body cavity. The larvae develop to the second instar in the host larva and complete development after the host pupates. The puparium is found in the host pupa. Strickland (1923) provides a detailed account of the life-cycle of a species he called *Gonia capitata*. King and Atkinson (1928) did not differentiate between three species of *Gonia* which they found but stated that as a group, they tended to select plants which were most likely to be eaten by host cutworms. None of these authors believed that *Gonia* species would ever show a high effective rate of parasitism in *E. ochrogaster* populations as has been found in *Agrotis orthogonia* Morrison populations.

When the cutworm is attacked by *Gonia* sp., the pupa darkens to a deep brown because of the presence of the puparium. The emerging adult causes a transverse break across the head

of the host pupa. (Fig. 62). The break usually closes and the host pupa remains intact. The abdominal segments remain very much like those of a normal pupa. In some specimens, the host pupa is expanded around the puparium and is slightly collapsed directly behind it.

Gonia aldrichi Tothill

King and Atkinson (1928) recorded *Gonia aldrichi* as reared from *E. ochrogaster*. They stated that *aldrichi* is the most important parasitoid of *E. ochrogaster* in the genus *Gonia* and is widely distributed in Saskatchewan. It appears that at least two species are currently included in the concept of *G. aldrichi* and both have been reared from *E. ochrogaster*. These species will be designated here as *G. aldrichi* No. 1 and *G. aldrichi* No. 2.

Description of puparia. — The puparia are similar in both of these species. The exit hole from the host pupa is a transverse, irregular break across the head of the pupa (Fig. 62). After the adult has emerged, the break is usually only slightly open except in the unusual cases where the anterior region of the host pupa is broken off. The posterior spiracles (Fig. 9, 10) are large and the orificial ridges are high and prominent. The orificial ridges occur very close to the edge of the spiracular plate and the ventral ridge often appears continuous with the edge. The cicatrix is usually poorly developed but varies in size and prominence from specimen to specimen. Spinules cover most of the puparium in indistinct bands. The spinules occur singly, and are randomly distributed (Fig. 11). The anterior spiracles have two very different shapes, one of which consists of two or three pori on a distinct pedicel (Fig. 8), and the other with 12 or more pori (Fig. 7) surrounding and partially obscuring the pedicel. The difference in anterior spiracle shape could not be correlated to other characters. Also, the number of pori vary on the same specimen though never from one type to the other.

Description of larvae. — The main difference between the two species lies in the shape of the cephalopharyngeal structures. The entire structure of *G. aldrichi* No. 1 (Fig. 5) is a wider triangle than that of *G. aldrichi* No. 2 (Fig. 6). The angle between the dorsal and ventral arms of the posterior sclerite is greater in No. 1 than in No. 2. The inner angle of No. 1 is only lightly, if at all sclerotized, whereas in No. 2 a definite band of up to one-quarter the width of the dorsal arm extends around the inner angle from near the tip of the dorsal arm to past the widened area of the lower arm. The lower arm of No. 1 lacks any definite widening along its length. The fused anterior and median sclerite of No. 1 is shorter than that of No. 2. The blade of the mouth hooks of No. 2 has a definite S-curve shape whereas in No. 1 the curve is a simple arc. The overall sizes of No. 1 and 2 are similar.

The second instar larvae of *Gonia* sp. (Fig. 12) were found in my dissections of dead host larvae. As the puparia and cephalopharyngeal structures of all the reared specimens were similar to the two *G. aldrichi* species, it is safe to call these second instar larvae *G. aldrichi* also. The cephalopharyngeal structures of these larvae are fused into a single sclerite (Fig. 13). The larva is 5 to 6 mm long, curved ventrally and patterned by black papillae. The patterns of papillae were not constant.

Biology. — While no adults were obtained from reared specimens in my study, several puparia were found in reared host pupae. The reared *Gonia* puparia compared favorably with borrowed specimens. It is likely that faulty rearing conditions caused the failure of adult emergence. During the dissection of dead host larvae, five specimens were found to contain from one to five second instar *Gonia* larvae. In one of these host larvae, two of the five *Gonia* larvae were damaged and partially disintegrated, while in another only the cephalopharyngeal structures of a larva were found, as well as a healthy *Gonia* larva.

Hosts. — Specimens of *G. aldrichi* examined were reared from *E. ochrogaster* and *A. orthogonia*.

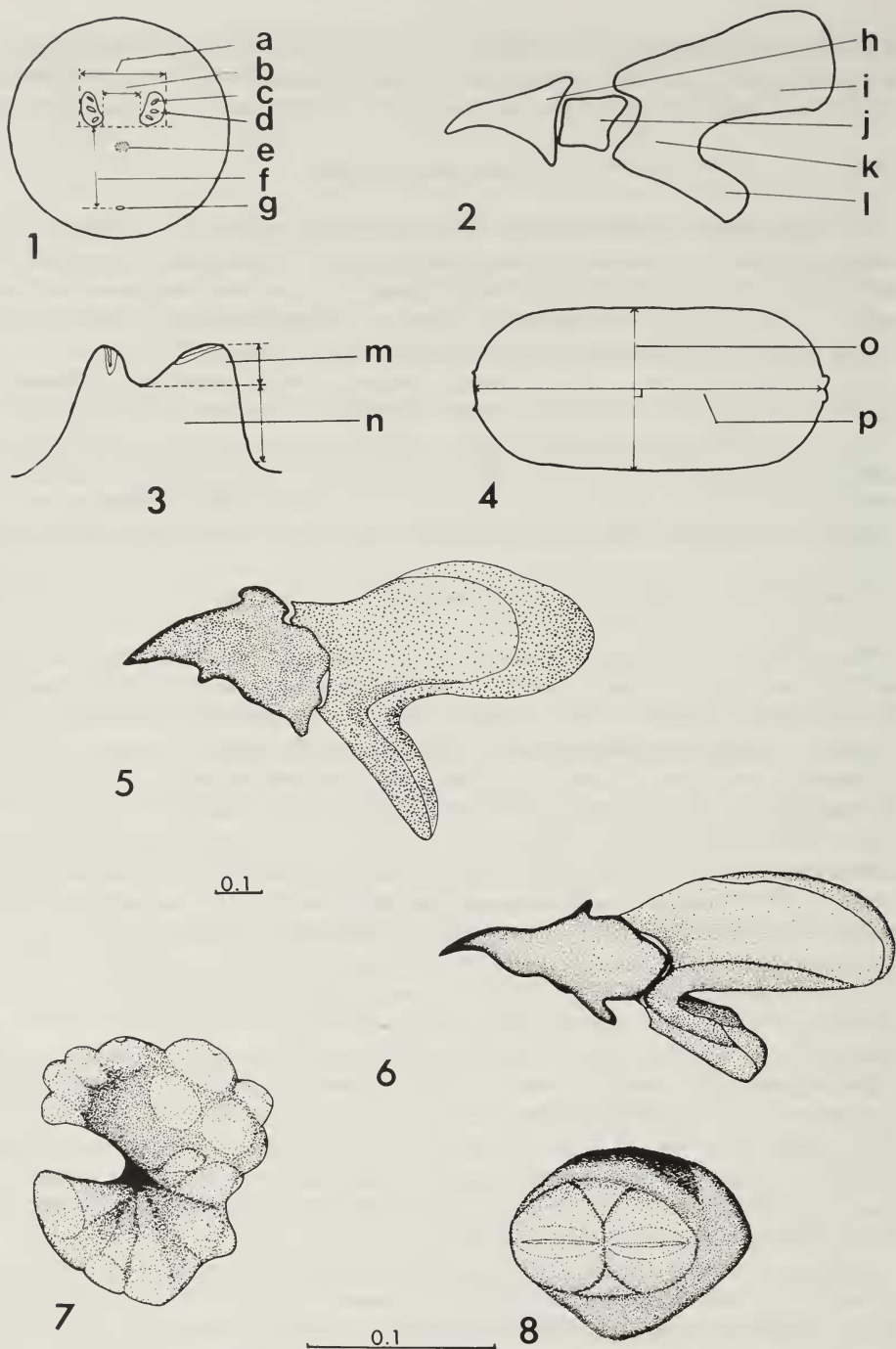


Fig. 1-4. Immature tachinids. 1. posterior view of puparium. a, b, maximum and minimum distance between posterior spiracles; c, orificium; d, spiracular plate; e, supra-anal protuberance; f, distance of anus from posterior spiracles; g, anus. 2. cephalopharyngeal structures of 3rd instar larva. h, anterior sclerite; i, dorsal process of posterior sclerite; j, median sclerite; k, posterior sclerite; l, ventral arm of posterior sclerite. 3. side view of posterior spiracle. m, orificial ridge; n, stigmatophore; (from Zuska, 1963). 4. dorsal view of puparium. o, p, width and length of puparium. Fig. 5-8. *Gonia aldrichi*. 5. cephalopharyngeal structures of *G. aldrichi* No. 1. 6. *G. aldrichi* No. 2. 7, 8. anterior spiracles. Scales in millimeters.

Gonia capitata (De Geer)

Gonia capitata was recorded as being reared from *E. ochrogaster* by Strickland (1923). Strickland noted that this could be a mistaken identification and that the species studied could be divided into five groups. It is now recognized that *G. capitata* is exclusively a European species (Brooks, 1943; Sabrosky and Arnaud, 1965). This invalidates the figures and descriptions of Greene (1921). The biological work of Strickland must now be regarded as being of *Gonia* sp. but is nevertheless a valuable source of information.

Gonia fuscicollis Tothill

Gonia fuscicollis was recorded as being reared from *E. ochrogaster* by King and Atkinson (1928). Brooks (1943) regarded this species as being so different from the other species of *Gonia* that he created the genus *Fuscigonia* for it. Unfortunately, no specimens were available for study.

Nothing is known of the biology of this species and it is likely that it is not an important parasitoid of any of the economic cutworms. The description of the immature stages is necessary in the future, however, to help separate the large number of species in this genus.

Gonia sequax Williston

Gonia sequax has not been recorded as being reared from *E. ochrogaster*. I am including *G. sequax* in this study as I am sure that it is a potential, if not actual parasitoid of *E. ochrogaster*, as well as to represent the *capitata* species group (Brooks, 1943).

Description of puparia. — The puparium of *G. sequax* is very similar to that of *G. aldrichi* in size and shape. The posterior spiracles (Fig. 15) differ in that the orificial ridges are set further in from the edge of the spiracular plate than those of *G. aldrichi*. The orificial ridges enclose the cicatrix which is fairly prominent. The anterior spiracles (Fig. 16) have only one porus on the end of a long pedicel. Only one specimen was examined so that this may not be characteristic of all members of this species. The spination of the puparia differs sharply from that of *G. aldrichi*. The spines (Fig. 17) tend to be in groups or series of three or more and often form long, irregular rows.

Description of larvae. — The cephalopharyngeal structures (Fig. 14) are similar to both *G. aldrichi* No. 1 and No. 2 but differ from both enough to be separated. The blade of the mouth hooks is a simple arc as in *G. aldrichi* No. 1 but the overall shape is closer to that of No. 2. Distinct from both *G. aldrichi* No. 1 and No. 2 is the anterior projection of the dorsal arm of the posterior sclerite. It is long, distinct, and well developed, and usually has a large open space between it and the anterior-median sclerite.

Biology. — Little is known of the biology of this species and how it differs from other members of the genus.

Hosts. — This species has been reared from *Agrotis orthogonia* from Alberta and Saskatchewan.

Bonnetia comta (Fallen)

The puparia and posterior spiracles of *Bonnetia comta* were described by Greene (1921) and all the life stages including the above structures were described by Strickland (1923). Allen (1926) described the first instar larvae. Greene's drawings either are not clear enough or are of a different species than what is now called *B. comta*.

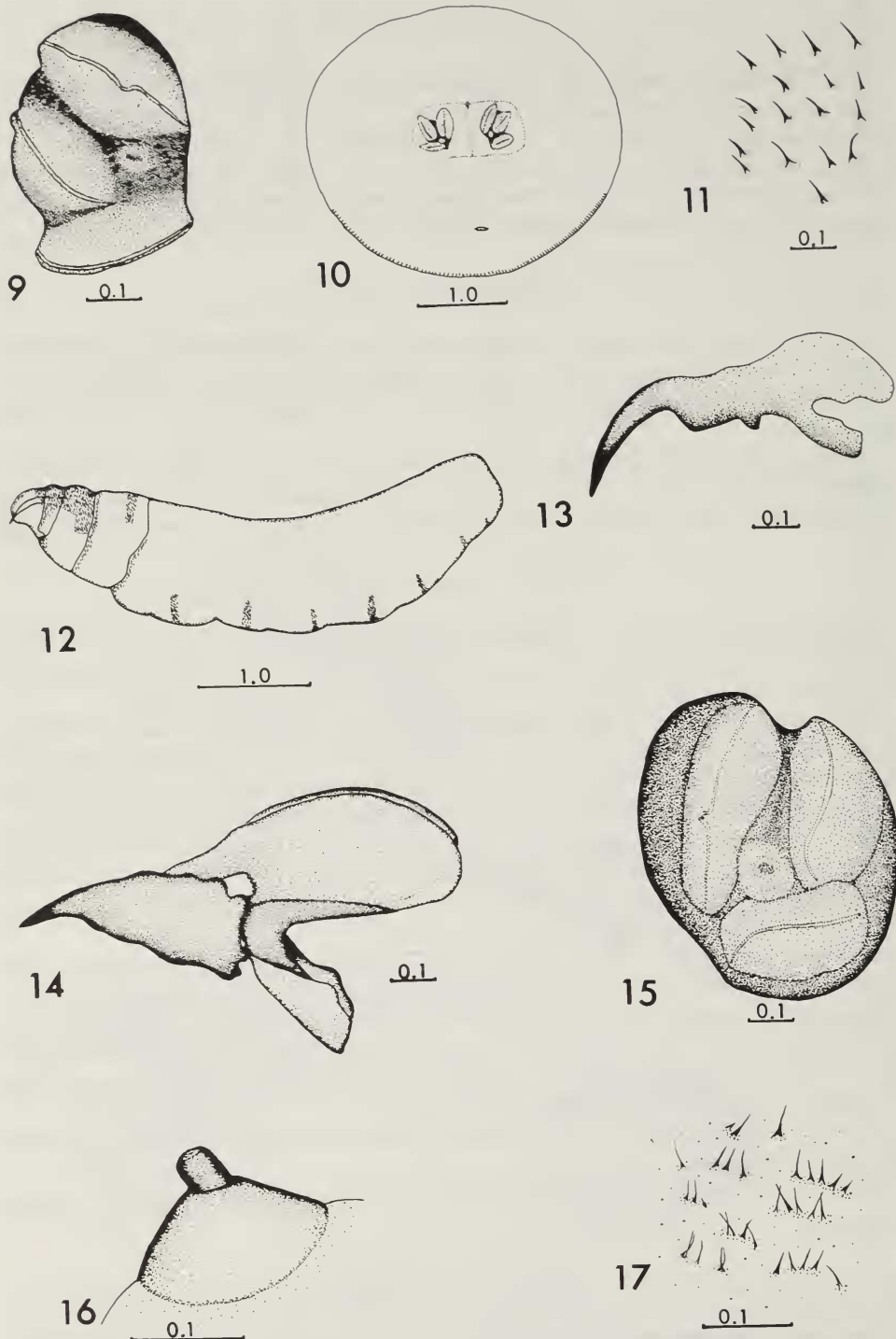


Fig. 9-13. *Gonia aldrichi*. 9. posterior spiracle. 10. posterior view of puparium. 11. spine pattern of puparium. 12. second instar larva. 13. cephalopharyngeal structures of second instar larva. Fig. 14-17. *Gonia sequax*. 14. cephalopharyngeal structures. 15. posterior spiracle. 16. anterior spiracle (side view). 17. spine pattern of puparium. Scale in millimeters.

Description of puparia. — The puparia are large, sub-elliptical, smooth-surfaced without any trace of spination, and show only vague segmentation marks (Fig. 22). The anterior stigmata (Fig. 20) are raised and show either five or six pori which are arranged in a curvilinear pattern with the axes of the individual porus pointing towards the center of the curve. Both the stigmatal plates and the supraanal protuberance are widely separated from the true anus and occur high on the dorsal surface of the puparium (Fig. 21). The stigmatal plates of the posterior spiracles (Fig. 19) are low and flat with the orificial ridges being only slightly raised but quite wide. The cicatrix is also low but is large and distinct. Occasionally, especially with transmitted light, a weakly sclerotized region can be seen between the inner and medial orificial ridges. The supraanal protuberance is pronounced and in some specimens is higher than are the stigmatal plates. From it runs a distinct ridge which separates the stigmatal plates.

Description of larvae. — Strickland (1923) describes the life stages and gives figures for them. The following passage is taken from his paper to describe the final instar larvae, which I have not examined.

"The smallest specimen seen measures 12 mm. long and 4 mm. wide; the largest, which was almost mature, was 15.75 mm. by 4.25 mm. While living, the larvae that were dissected from their host constantly changed their shape by violent muscular contractions. The transparent cuticle revealed the yellow and brown viscera in strong contrast to the voluminous white fat-body. When killed . . . the larva is arcuate, dorsum concave, tapering cephalad and slightly so to the bluntly rounded caudal extremity. Eleven segments, only, were seen. Dorso-laterally between segments I and II there are a pair of blackened spiracles . . . each of which possesses six respiratory papillae that open into a short constricted felt-chamber, behind which are a pair of stout trachea which run the length of the body and connect with the caudal spiracles. The cuticle is almost destitute of armature, though minute simple spines are present on all of the intersegmental areas. These are most numerous in the anterior and posterior segments where they form a fine network of rows that encircle the body. In addition there are traces of intersegmental hooks between the four anterior segments. The buccal-pharyngeal armature . . . differs little from that of the preceding stage except in size. The over-all measurement is 1.0 mm. to 1.1 mm., the mandibular hooks being 0.17 mm. to 0.18 mm. long."

Strickland's drawings of the cephalopharyngeal structures provide the appropriate general impressions but are inaccurate in one aspect. Ventral to the anterior sclerite lies an auxiliary sclerite as shown in Fig. 18. This sclerite is always shown as being solidly fused to the anterior sclerite in Strickland's paper. I have examined 12 borrowed specimens and three slides which were part of Strickland's study and my interpretation is as follows: The posterior sclerite is very slightly sclerotized and while it has a characteristic shape, it is often twisted or bent in the puparium. The anterior process of this structure becomes progressively less sclerotized until it terminates in a ligament-like structure which connects with the posterior process of the anterior sclerite. The articulation between the median and posterior sclerite is very weak and usually releases when the entire structure is being removed from the puparium. In contrast, the anterior articulation is very solid and it is often difficult to find the division between the two sclerites except at the tip of the posterior process of the anterior sclerite.

Biology. — The life history and behavior of *B. comta* is well outlined by Strickland (1923). This species belongs to the tachinids which either larviposit or oviposit in an area where the first instar larvae can actively attach themselves to a host and enter from the outside of the body. Strickland found that the cutworms were attacked in the third or fourth instar and death resulted during the prepupal stage when the mature larva emerged to enter

the soil and pupate.

Hosts. — Two generations occur per year with the larvae of the second generation overwintering in their hosts. The hosts recorded for this species in Strickland's (1923) paper are as follows: *Euxoa tristicula* Morrison, Montana; *E. messoria* Harris, Washington; *Agrotis ypsilon* L., California; *A. orthogonia* Morrison, Alberta; *Copablepharon viridisparsa* Dod., Alberta; *Polia acutetermina* Sm., Alberta (induced parasitism). King and Atkinson (1928) recorded *B. comta* as reared from *E. ochrogaster* but found it to be an insignificant parasite during their studies in Saskatchewan.

Periscepsia Gistel

This genus has been handled in several different ways by various authors. Sabrosky and Arnaud (1965) list six different synonyms of *Periscepsia*. The confusion with regard to *P. helymus* and *P. laevigata* lies in the fact that the former has been placed in seven different name combinations and the latter in eight. In addition, many authors confused *P. laevigata* with *P. helymus* and named it as the latter. The major generic names in which both species have been placed and which have been used in the literature are *Phorichaeta*, *Metachaeta*, and *Wagneria*. *P. helymus* has also had the specific names *helyma* and *sequax*, while *P. laevigata* has been known as *helymus*, *atra*, and *carbonaria*. The character recognized by Reinhard (1955) and Wood (pers. comm.) to separate these species is the presence of setae on the median portion of the first wing vein in *P. laevigata* as opposed to a bare first wing vein in *P. helymus*. Because of the confusion which has existed about these two species, one must regard the host lists from the literature with caution.

Periscepsia helymus (Walker)

The puparia of *P. helymus* were described by Greene (1921) under two synonymous names, *Phorichaeta sequax* (Williston) and *Metachaeta helymus*, but the puparia were different from each other.

Description of puparia. — Greene's (1921) descriptions and figures of the puparia under the name *Metachaeta helymus* closely resemble *P. helymus*, while those of *Phorichaeta sequax* differ sufficiently from the other two to be considered different. Also, the puparia which I measured were significantly larger (4.5 x 2.1 mm) than the dimensions given by Greene for *Phorichaeta sequax* (3.5 x 1.5 mm). Even the ranges of the specimens I studied (4.08 mm - 4.88 mm x 1.92 mm - 2.16 mm) did not include his dimensions. *M. helymus* dimensions were 4.75 mm x 1.75 mm and hence are similar to the measurements taken from my study series.

From a lateral view of the puparium, the posterior regions carrying the stigmatal plates and anus appear extended (Fig. 24). From a posterior view the puparia appear nearly circular with a raised central region (Fig. 25). The spiracular plates are terminal in position. The spiracular plates of the posterior spiracles (Fig. 26) are narrowly separated, only slightly raised and are quite flat. The cicatrix is large, round, and slightly concave in the central region. The entire shape of the spiracular plate varies from oblong to slightly curved. The anterior spiracles are especially poor characters in this group because they are often lost at emergence. The stigmata are small and tuberculate with a cluster of pori in a crescent (Fig. 28). The number of pori is not constant.

Description of larvae. — No specimens of the final instar larvae were available for study, therefore I am relying on the cephalopharyngeal structures recovered from the puparia for characters. The cephalopharyngeal structure (Fig. 23) is very distinctive but the variations

which occur tend to confuse its appearance. The anterior sclerite is heavily sclerotized with the ventral process being almost as long as the actual mouth hooks. Behind the ventral process lies an auxiliary sclerite which may be concealed or lie in several different positions in the same general region. The median and posterior sclerites are fused but with adequate lighting, the suture can be seen. Projecting dorsally from the median sclerite is a hook-like process which curves anteriorly. The posterior sclerite varies considerably in the degree of sclerotization from a dark colour which nearly obscures the hook, to a very weakly sclerotized, clear structure. In the latter case, many structural differences appear but are probably insignificant. In this species the anterior process of the posterior sclerite is very weak or lacking. In some specimens a membranous connection may be seen between the anterior and posterior sclerites in the dorsal regions.

Biology. — Little is known of the biology of this species except that it attacks cutworm larvae and that more than one may emerge from a single host (Reinhard, 1955). Guppy (1967) records three or four *P. helymus* as being reared from a single sixth instar *P. unipuncta* Haworth larva.

Hosts. — In the literature, *P. helymus* has been recorded as reared from the following hosts: *Heliophila commoides* Guenée (Tothill, 1913), Ontario; *Pseudaletia unipuncta* Haworth (Baker, 1914), Ontario; *Euxoa ochrogaster* (King and Atkinson, 1928), Saskatchewan. Reinhard (1955) lists the following hosts not recorded above: black army cutworm, *Actebia fennica* Tausch, Michigan; *Peridroma saucia* Hübner, California; *Cirphis* sp. Hampson, Washington; *Euxoa auxiliaris*, Alberta; *Polia adjuncta*; *Grapholitha* sp. *Conistra devia* Grote; *Lithophane innominata* Smith, Maine. Specimens which I examined were reared from: *H. commoides*, Ontario; *A. eliminata* Gn., New Brunswick; *Rhynchagrotis cupida* Grote, New Brunswick; *Andropolia vancouvera* Strand, British Columbia; *Andropolia* sp. Grote, Alberta; *A. contacta* Walker, Alberta.

Periscepsia laevigata (Van der Wulp)

There appears to be no previous description of the immature stages of this species in the literature.

Description of puparium. — Only the puparium of one specimen was studied and it lacked the anterior flaps so that neither the cephalopharyngeal structures nor the anterior spiracles were available for study. The posterior spiracles are similar to those of *P. helymus* but the orificial ridges tend to be higher, wider, and more rounded (Fig. 27). The orificia follow the top of the ridges almost to the level of the spiracular plates. While the cicatrix is large and round it is not as distinct as that of *P. helymus*. The best differentiating character is the median orificium which is very curved in *P. laevigata* but nearly straight in *P. helymus*. The rounded shape of the orificial ridge of *P. laevigata* contrasts well with the long, narrow shape in *P. helymus*.

Biology. — Little is known of the biology of this species except that it attacks fifth instar cutworm larvae (Guppy, 1967). The range of the species is from Guatemala to Canada (Reinhard, 1955).

Hosts. — The problem of host records is important in regards to this species. As one cannot be sure of the accuracy of earlier identifications, it is possible that the following list is either incomplete or inaccurate. Reinhard (1955) lists the following hosts: *Pseudaletia unipuncta*, *Euxoa auxiliaris*, *Grapholitha* sp. Hübner; *Lascoria ambigualis* Walker, *Elaphria nucicolora* Grote, and unidentified cutworms. Guppy (1967) records *P. unipuncta* from Ontario as a host. The specimen I examined was reared from an unidentified 'phalaenid' from Big Beaver, British Columbia.

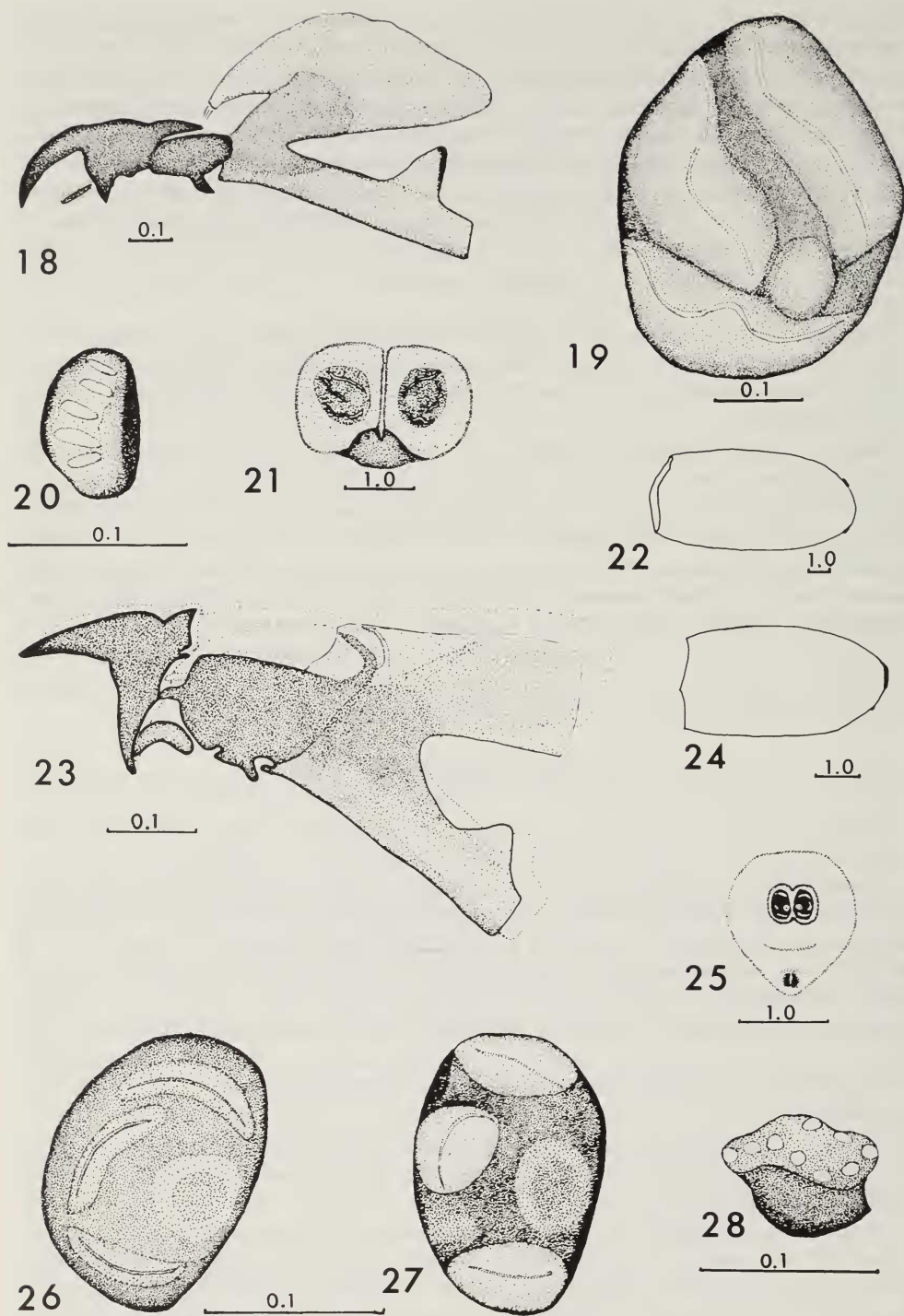


Fig. 18–22. *Bonnetia comta*. 18. cephalopharyngeal structures. 19. posterior spiracle. 20. anterior spiracle. 21. posterior view of puparium. 22. puparium. Fig. 23–26, 28. *Periscepsia helymus*. 23. cephalopharyngeal structures. 24. puparium. 25. posterior view of puparium. 26. posterior spiracle. 28. anterior spiracle. Fig. 27. Posterior spiracle of *P. laevigata*. Scale in millimeters.

BOMBYLIIDAE

Biology and morphology of immature bombyliids

Five species in two genera of Bombyliidae have been recorded as primary parasitoids, and one other species as a hyperparasitoid of *Euxoa ochrogaster*. Brooks (1952) illustrated the final instar larvae and the pupae of five of these six species and provided keys for their identification. Painter and Hall (1960) provide keys for adults to the genera of Bombyliidae, to the subgenera of *Villa*, and to the known species of *Poecilanthrax*. Generally, little is known of the biology of bombyliids. No comprehensive work has been done on the biology of any species attacking Lepidoptera. The terminology used for the morphology of the immature stages is based on Berg (1940) in his work on the immature stages of *Systoechus vulgaris* Loew.

While Bohart *et al.* (1960) suggest that there may be four larval instars, other authors have only described three (Hynes, 1947; Berg, 1940; Clausen, 1928). The first instar larva is active, vermiform, and adapted to move through the soil and seek out its host (Clausen, 1928; Bohart *et al.*, 1960; Berg, 1940). In parasitoid species the first instar larvae penetrate their host and develop internally. The second instar larva is far less mobile than the first and is more maggot-like (Clausen, 1940; Bohart *et al.*, 1960). It has lost its adaptations for moving through the soil and likely can only move in open areas. In species which are internal parasitoids, the larva likely molts immediately after attacking the host due to the radically different environment in which it then lives. Because the cast skin of the final instar larva can be found in the pupal case of the host, descriptions of this stage are available for several species. Brooks (1952) reviews the taxonomically important characters of both the final instar larvae and the pupae of noctuid-attacking bombyliids. In the final instar larvae he found the structure of the mouth parts and the head sclerites to be important. In the pupae he found that the head tubercles and mouth part sizes were of specific use, whereas the apical segments were of little use due to the general uniformity in the group and the variability within the species involved.

Bombyliids have been observed apparently ovipositing in loose sand or dust, but this has not been confirmed (Painter and Hall, 1960). Brooks (1952) noted that the species attacking noctuids fly from the latter half of July through to September, but the hosts are not attacked until their fourth, fifth or sixth instars the next season. He felt that the species overwinters as eggs in the soil or old vegetation. Painter and Hall feel that the first instar larvae seek out small caterpillars as hosts and remain inactive until the host pupates, when they rapidly develop and kill the host. The bombyliid pupa breaks out of the host pupal remains, and with the use of directed spines and bristles moves to the soil surface where the adult emerges quickly (Painter and Hall, 1960; Allen, 1921; Snow, 1925). It is likely that the abrasion from moving through the soil accounts for much of the intraspecific differences which have been observed in the shape of the head tubercles, apical segments, and spines.

Other than Allen's (1921) report that *Poecilanthrax lucifer* (Fabr.) attacked 25% of the fall army worm, *Spodoptera frugiperda* (Smith) in Mississippi, bombyliids have been regarded as minor parasitoids of noctuids (Brooks, 1952; King and Atkinson, 1928).

Villa Lioy

This genus has a wide host range as internal or external parasites of Diptera, Lepidoptera, Hymenoptera, and Coleoptera. Painter and Hall (1960) provide a key to the adult subgenera. Two of these, *Villa* and *Hemipenthes*, are of interest to us.

Villa (Villa) alternata (Say)

This species was recorded by Brooks (1952) as a parasite of *E. ochrogaster* which was collected as fourth, fifth, and sixth instar larvae in May and June. Records show this species to range across the prairies of Canada. Brooks provides illustrations of the mouth hooks, head capsule, and apical platelets of the mature larvae as well as of the entire pupa, its head, and apical structures.

Hosts. — *Euxoa flavicollis* Sm., *E. tessellata* Harris, *Agrotis orthogonia*, *Feltia ducens* Walker, *E. ochrogaster*, (Brooks, 1952); tenebrionid larvae (Clausen, 1940).

Villa (Villa) fulviana (Say)

This species was recorded by King and Atkinson (1928) as reared from *E. ochrogaster*, but only from *Euxoa* sp. Hübner by Brooks (1952). It has been collected in host pupae from June 30 to July 12 and found to emerge as adults in the autumn. King and Atkinson felt that it overwinters in alternative hosts. Illustrations of the larvae and pupae are provided by Brooks.

Hosts. — *E. ochrogaster* (King and Atkinson, 1928), *Euxoa* sp. Hübner (Brooks, 1952).

Villa (Villa) lateralis (Say)

King and Atkinson (1928) record this species as having attacked two specimens of *E. ochrogaster* and emerging in the autumn. No reference is made to this species by Brooks (1952). No drawings of any of the life stages are known and no material appears to be available at the present time.

Villa (Hemipenthes) moroides (Say)

Species of the subgenus *Hemipenthes* are hyperparasitic upon the primary parasites of Lepidoptera (Clausen, 1940). Clausen refers to members of this subgenus as attacking ichneumonid parasitoids, but Brooks (1952) records three species as reared from tachinid hosts. *V. moroides* was reared from *Gonia* spp. and *Bonnetia comta*, which were reared from noctuid hosts. Clausen stated that the exact relationship between the host, parasitoid, and hyperparasitoid was not established and that it was possible that the ichneumonids were attacked in the pupal stage independently of the host. It appears that a true hyperparasitoid role has been established for *V. moroides*.

Poecilanthrax Osten Sacken

This is a widespread genus which attacks chiefly noctuid larvae. Painter and Hall (1960) list 15 species of cutworms and army worms which are attacked by eight species of *Poecilanthrax*.

Poecilanthrax alcyon (Say)

This species was recorded as a parasitoid of *E. ochrogaster* by King and Atkinson (1928) under the name of *halcyon*. Painter and Hall (1960) give the distribution of the species in southern Canada and the United States, but fail to show the correct boundaries of northern distribution. The range extends from Texas to the Northwest Territories, and with the ex-

ception of Southern California, east of the Rocky Mountains to the Atlantic Ocean.

Brooks (1952) illustrated the final instar larva (Fig. 32) and pupa. Painter and Hall (1960) discuss the entire species at length, as *P. alcyon* is the type of the genus, and give a detailed description of the adult. Fig. 29, 30, 31 and 33 are original drawings of a specimen of *P. alcyon* reared from *E. ochrogaster*.

Only one specimen of a pupa attacked by *Poecilanthrax alcyon* (Fig. 63) was examined. This specimen was a light brown similar to one from which a moth had emerged. The adult *P. alcyon* emerges from the dorsal surface behind the head, leaving the pupa intact. The abdominal segments are fully extended after emergence.

Hosts. — *E. ochrogaster*, *E. flavicollis*, *Chorizagrotis thanatologia*, *Pseudaletia unipuncta*, (Brooks, 1952); *peridroma margaritosa* (Walkden, 1950).

Poecilanthrax willistonii (Coquillett)

The adults of this species were reported by King and Atkinson (1928) to emerge either in the autumn or the following June. They felt that the species overwinters as larvae in noctuid hosts which overwinter in the larval stage. Painter and Hall (1960) show the distribution as from south of the United States to the middle of the prairie provinces of Canada, and from the west coast through to the central great plains. Figures of the larvae and pupae are given by Brooks (1952) and those of the pupae are reprinted by Painter and Hall (1960).

Hosts. — *Agroperina dubitans* Walker, *Chorizagrotis thanatologia* Dyar, *S. devastator*, *Euxoa flavicollis*, *E. ochrogaster*, *E. tessellata*, *Feltia ducens*, (Brooks, 1952); *Chorizagrotis auxiliaris* Grote, *Euxoa scandens* Riley, (Walkden, 1950).

ICHNEUMONIDAE

Morphology of immature ichneumonids

The ichneumonid parasitoids have many taxonomic characters which are useful to separate their immature stages. The terminology and approach to description follows that of Finlayson (1960). The cocoons, if present, can be separated using: size, color and shape, and location of the adult emergence hole from the cocoon. The spiracles were of limited use when studying these species as the differences I found were insignificant. The best separating characters for the final instar larvae were found in the cephalic structures (Fig. 34). To differentiate between species, the presence or absence of sclerites, and the shape of mandibles were the best characters found.

Preparation of specimens. — After having been soaked in water for at least 24 hours, the final instar larval skins were removed from the cocoons by means of fine forceps or a hooked pin. The larval skin was gently unfolded and removed from the adult meconium which covered many of the specimens. The skin was then placed in 10% KOH for 24 hours at room temperature, or longer if it was not cleared enough. Boiling in KOH was found to disarticulate the cephalic structures resulting in the loss of sclerites, and so was not used. The cleared larval skin was mounted in polyvinyl lactophenol on microscope slides for further examination. Polyvinyl lactophenol was chosen because it is a mild clearing agent and thus aids in the ease of sclerite recognition.

Four species of the tribe Ichneumonini have been recorded as parasitoids of *E. ochrogaster*. Three species, *Eutanyacra suturalis*, *Diphyus* No. 1, and *Spilichneumon superbus* were examined and found to be similar in the following ways. The females lay their eggs in the cutworm larvae but the host is not killed until it reaches the pupal stage. None spin any apparent cocoon and all use the host pupa for protection during their pupal stage. All have

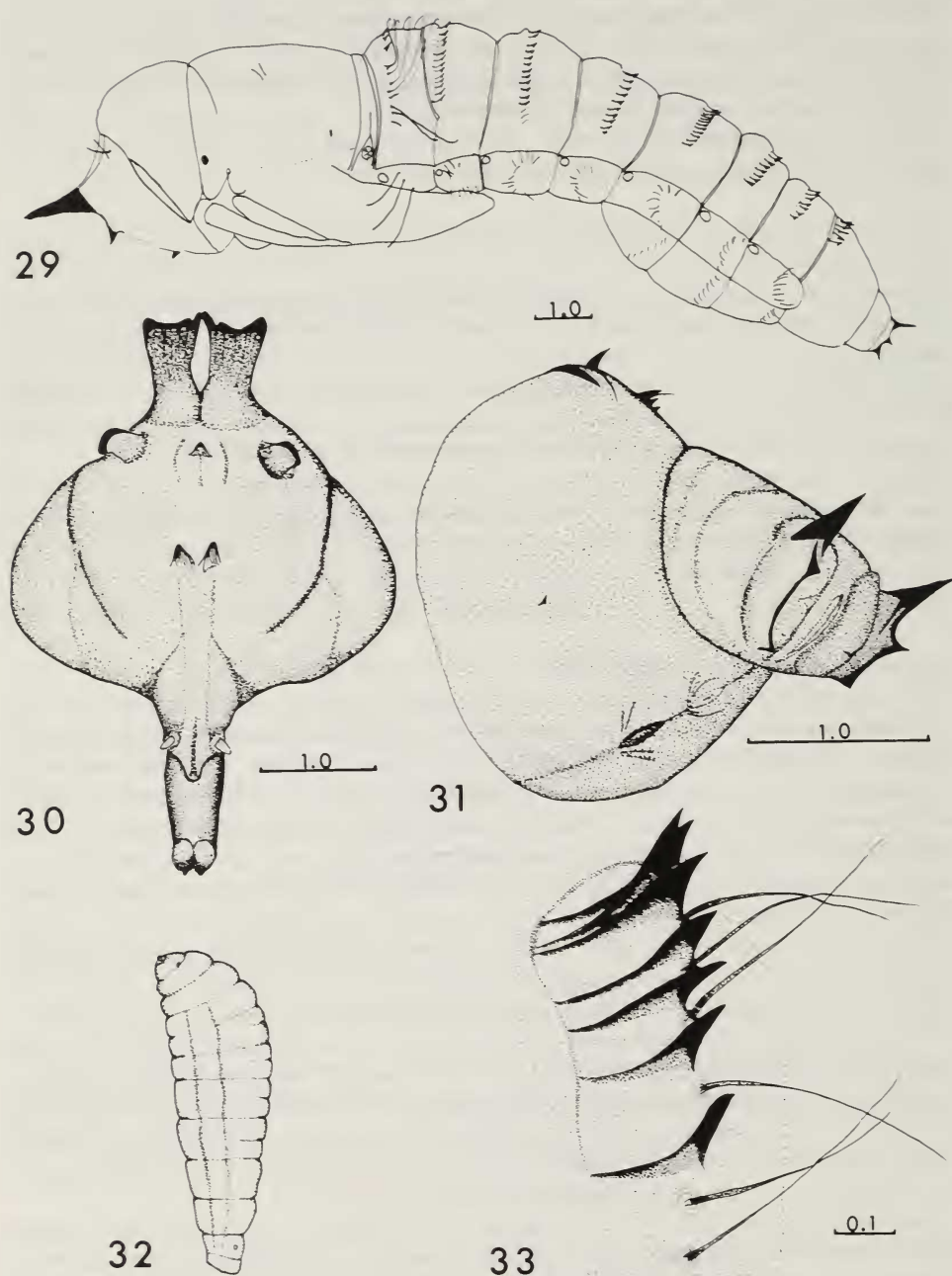


Fig. 29-33. *Poecilanthrax alcyon*. 29, pupa. 30, ventral view of pupal head. 31, ventro-lateral view of posterior end of pupa. 32, final instar larva (Brooks, 1952). 33, spine and setal pattern of third abdominal segment of pupa. Scale in millimeters.

greatly reduced larval mouth parts which differ between species mainly in the mandible shape. One pair of sclerites located behind the mandibles do not conveniently fit into the Finlayson (1960) sclerite classification. It is possible that these are modified from the suspensorial sclerite. In all these species, the stipital and labial sclerites are lost. The shape of the spiracles is quite constant (Fig. 37), and is of no use to separate species. Several ichneumonine larvae were dissected from final instar cutworm larvae and one was removed from a host pupa. Those removed from the cutworms were an early instar (Fig. 36) and could be either *Diphyus* No. 1 or *S. superbus*. The one removed from the pupa had cephalic structures which were clearly those of *Diphyus* No. 1. When attacked by any of these species, the host pupa does not darken as it normally does, but remains the shiny brown of a healthy 3 to 7 day old pupa. The anterior portion of the host pupa is chewed and broken by the emerging ichneumonine adult (Fig. 64). The pupal remains are distinct from those from which a moth has emerged (Fig. 61). The unexamined species, *Pseudamblyteles subfuscus*, is likely similar to the examined species.

Eutanyacra suturalis (Say)

Description of larvae. — The cephalic structures (Fig. 35) of the final instar larva with incomplete epistoma. Pleurostoma wide, heavily sclerotized, and with a very irregular, poorly defined edge. Superior mandibular process wide and short, inferior mandibular process reduced to one. Pleurostoma and hypostoma closely connected but limited movement between them possible. Hypostomal arms heavy and of irregular width. Stipital and labial sclerites missing. Labial and maxillary palpi small and difficult to see. Silk press small and very lightly sclerotized. Mandibles large, robust, heavily sclerotized with slightly curved blades which continued into base without clear marking. Behind or above mandibles, the two sclerites heavily sclerotized and irregularly larger dorsally than ventrally.

Biology. — *E. suturalis* females were observed, collected, and reared during the *Actebia fennica* outbreak at Worsley, Alberta in 1967. The females were seen to fly and hunt during the late afternoon and early evening. They were found hunting in fields which had been defoliated several days before by the passing cutworm army. The hunting females ran rapidly on the soil surface and searched around soil clods and in large cracks in the soil. While hunting, they could be easily approached and could be captured by hand. Captured females would attack field-caught *A. fennica* larvae, but oviposition was never observed. The attack consisted of mounting the cutworm lengthwise and curling the tip of the abdomen under so that the ovipositor touched the cutworm. At this point, every attacking female was flipped off the cutworm by a violent twisting movement of the cutworm. In no instance was such a cutworm reattacked, and I never succeeded in rearing an *E. suturalis* adult from an offered cutworm. In the laboratory, adult *E. suturalis* emerged 10 to 14 days after host pupation.

Hosts. — Whitehouse (1922) recorded *E. suturalis* as reared from *E. ochrogaster* in Alberta. The following hosts were found by examining host labels in the C.N.C.: *Actebia fennica*, British Columbia; *E. ochrogaster*, Saskatchewan; *E. flavicollis*, Saskatchewan; *Scotogramma trifolii* Rottenburg, Saskatchewan.

Spilichneumon superbus (Provancher)

Description of larvae. — The cephalic structures of the final instar larva (Fig. 39) are similar to those of *E. suturalis* and *Diphyus* No. 1. The size is closer to that of *Diphyus* No. 1 than to that of *E. suturalis*. The mandibles are short and broad with a wide, straight

blade which is continuous in appearance with the base. The edge of the pleurostoma is well defined as in *Diphyus* No. 1.

Biology. — This species was reared from *A. fennica*, *E. ochrogaster* and *F. ducens* during the current study. Because it was not recognized as being different from *Diphyus* No. 1 while live adults were available, the adults were mixed and little data on either behavior or biology was obtained. The adults emerged from the host about 3 weeks after host pupation.

Hosts. — The following hosts of *S. superbus* have been recorded (Heinrich, 1960): *Chorizagrotis auxiliaris*, Alberta; *E. ochrogaster*, Manitoba; *E. scandens*, *E. flavicollis*, *E. messoria*, *Feltia ducens*, Saskatchewan; *Pseudaletia unipuncta*, Hawaii (introduced).

Pseudamblyteles subfuscus (Cresson)

Strickland (1923) recorded *Amblyteles subfuscus* as reared from *E. ochrogaster*. This species was subsequently transferred to *Pseudamblyteles* which is now considered to be congeneric with *Diphyus* Kriechbaumer (Heinrich, 1961). The genus *Diphyus* is now being reworked and the different species are currently denoted by numbers in the C.N.C. In the C.N.C. only *Diphyus* No. 1 of the genus *Diphyus* had host labels associating it with *E. ochrogaster*. Dr. Mason (pers. comm.) states that *Diphyus* No. 1 does not include what was *P. subfuscus*. There is no other evidence currently available to determine which of the *Diphyus* species was *P. subfuscus*.

Strickland (1923) described the biology of *P. subfuscus* from his research. Unfortunately little of the data which he presents is of use to separate *P. subfuscus* from any of the other ichneumonines which attack *E. ochrogaster*. The major biological fact which he describes is that the eggs are laid in the salivary glands of the host cutworm. During my dissections of *E. ochrogaster* larvae, I have seen neither the eggs which he describes nor the resulting scar on the salivary glands. Until the taxonomy of *Diphyus* is better understood, the status of *P. subfuscus* as a parasitoid of *E. ochrogaster* will be unclear.

Hosts. — Strickland (1923) reared *P. subfuscus* from *Chorizagrotis auxiliaris* and *E. ochrogaster* in Alberta, while Gibson (1917) reared it from *Euxoa excellans* Grote in British Columbia.

Diphyus No. 1

Description of larvae. — The cephalic structures of the final instar larvae (Fig. 38) of *Diphyus* No. 1 are similar to those of *E. suturalis*. The mandibles differ from those of *E. suturalis* in that they have a long narrow blade which is well marked off from the base. When rotated the blades appear to be curved posteriorly. The sclerites above the mandibles tend to be more squared than those of *E. suturalis*. The edge of the epistoma in *Diphyus* No. 1 is well defined.

Biology. — Using the final instar cephalic structures, it was found that this species was a parasitoid of *E. ochrogaster* at Calahoo. Adults emerged from the host pupae about 3 weeks after host pupation.

Hosts. — The following hosts were found by examining *Diphyus* No. 1 specimens in the C.N.C.: *E. ochrogaster*, Alberta; *C. auxiliaris*, Alberta; unidentified cutworm, British Columbia.

Campoletis atkinsoni (Viereck)

King and Atkinson (1928) reported *C. atkinsoni* as reared from *E. ochrogaster*. This

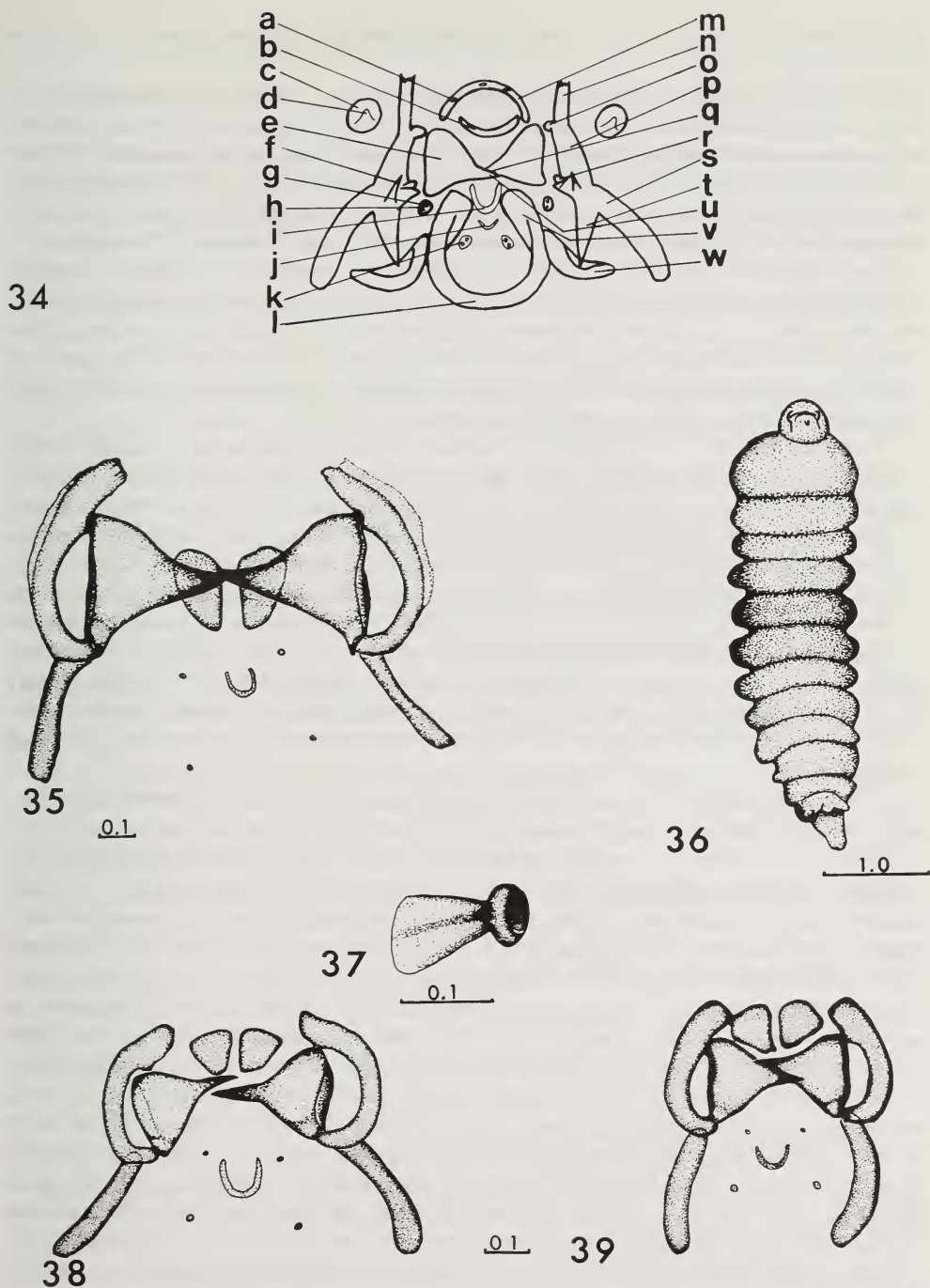


Fig. 34. Generalized cephalic structures of final instar ichneumonoid larva (from Finlayson, 1960). a, vacuole; b, suspensorial sclerite; c, antennal socket; d, antenna; e, mandible; f, lacinial sclerite; g, sensorium; h, maxillary palp; i, silk press; j, prelabial sclerite; k, labial palp; l, labial sclerite; m, labral sclerite; n, epistoma (incomplete); o, superior mandibular process; p, pleurostoma; q, teeth; r, inferior mandibular process; s, hypostoma; t, hypostomal spur; u, blade of mandible; v, dorsal arm of labial sclerite; w, stipital sclerite. Fig. 35. Cephalic structures of final instar larva of *Eutanyacra suturalis*. Fig. 36. Ichneumonine larva. Fig. 37. Larval spiracle of *Spilichneumon superbus*. Fig. 38. Cephalic structures of final instar larva of *Diphyus* No. 1. Fig. 39. Cephalic structures of final instar larva of *S. superbus*. Scale in millimeters.

species appears to be one of the more important parasitoids of *E. ochrogaster*. This will be discussed later.

Description of cocoon. — The cocoon (Fig. 40) (2.1-2.4 x 5.4-6.2 mm) consists of two layers: a very thin outer layer of silk which is also used to secure the cocoon to the substrate, and a tough inner parchment-like layer. The freshly spun cocoon is a light yellowish white but the mature cocoon varies from a dark tan to a dull brown. Some of the specimens reared in this study were observed to spin their cocoons with the host remains attached to the posterior end. In other cases, the larva would crawl a few centimeters before spinning a cocoon. In all cases the cocoon took 12 to 18 hours to complete. The exit hole is on the dorsal edge of the anterior end of the cocoon. It is irregular in outline as the adult chews its way out. The remains of the final instar larva are stuck to one side near the end of the cocoon. These remains are often difficult to find and remove. The remains of the pupa and the meconium tend to obscure the larval remains so that care must be taken not to lose the cephalic structures in any of the study procedures.

Description of larva. — The cephalic structures of the final instar larva (Fig. 42) with a complete epistomal arch which is very lightly sclerotized and difficult to recognize. Superior mandibular processes sclerotized and small. Inferior mandibular processes well developed. Lacinial sclerite absent. Hypostoma long, narrow, straight, and heavily sclerotized. Hypostomal spur about 1½ times as long as wide at base and meets straight, well-developed stipital sclerite at about midpoint. Stipital sclerite meets top of labial sclerite. Labial sclerite widest at one-third of way from base and narrowed to a rounded point at end. End of labial sclerite very lightly sclerotized and may appear lost. Silk press large, wide, well developed and terminated by a long narrow spur. Mandibles small with a short blade which curves directly from base. Labral sclerite absent. Suspensorial sclerite short and narrow. Maxillary palpi large and well developed and protrude in a large membranous sack. Antennae large and well developed.

Biology. — *C. atkinsoni* is the only recorded parasitoid of *E. ochrogaster* which attacks the early instar larvae. It usually kills the host in the third or fourth instar. For this reason, this species is usually overlooked or not found in studies based solely on outbreak conditions. The first evidence of the presence of a *C. atkinsoni* larva in a host appears 2 to 4 days before the host is killed. At this point, the host is noticeably more sluggish, eats less than normal, and tends to bulge abnormally. Subsequently, the host stops eating, loses its mobility, and begins to lose its normal shape. Just before the parasitoid emerges, it can be seen moving about in the host, as the host's integument is very limp. The *C. atkinsoni* larva devours the entire contents of the host so that after it rips its way out of the host, the remains lie very flat and are nearly transparent. The parasitoid larva begins to spin its cocoon immediately after emergence and usually needs some object to crawl against so that it can complete its cocoon. The cocoon is stuck to the substrate with silk fibers. The adult *C. atkinsoni* emerge 7 to 10 days after the completion of the cocoon. All the specimens studied in 1968 emerged from the host during the last few days of May and the first week of June, and the adults emerged during the first 3 weeks of June. Although all available cutworm species found in the test area were reared in both 1967 and 1968, no alternative host was found later in the season.

Hosts. — *E. ochrogaster* appears to be the only recorded host of *C. atkinsoni*. Graham (1965) lists several noctuid hosts of *Campoletis* spp. and one yponomeutid, the diamond-back moth, *Plutella maculipennis* Curtis. As *C. atkinsoni* attacks only the early instars of its cutworm hosts, its host range will likely only be found in studies which are based upon endemic cutworm populations rather than epidemic populations.

Netelia Gray

The genus *Netelia* formerly was named *Paniscus* Schrank. The name change was necessitated because of the misapplication of the name *Paniscus* by Gravenhorst (Townes *et al.*, 1961). Townes *et al.* provide taxonomic information on the adults of this genus and give keys and characters to separate specimens to the sub-generic level. Using his characters, it was found that the specimens reared from *E. ochrogaster* were in the sub-genus *Netelia*.

Description of cocoon. — The cocoons of three borrowed specimens of *Netelia* sp. were examined but none contained any larval remains. One cocoon found in the field study at Calahoo closely resembled those of *Netelia*, and it also lacked any larval remains. It is possible that the larval exuviae were removed from the borrowed specimens by a previous worker. It is also possible that the remains are left loose in the cocoon and easily lost. While the literature contains generalized descriptions of *Netelia* larvae, no mouth part drawings appear to be available. Cushman (1926) and Strickland (1923) provide illustrations of larvae and eggs of various members of the genus.

The cocoons studied averaged 4 x 12 mm in size. The cocoon (Fig. 41) consists of a very sparse outer covering of silk which appears as a fluffy mass at the ends, and a tough, tightly constructed inner layer. The over-all color is shiny black, but Strickland (1923) noted that it is originally a light color which changes with maturity. When viewed laterally, the cocoons had a slightly curved shape. The adults emerged from the end of the cocoon leaving a very ragged and irregular exit hole.

Biology. — *Netelia* sp. is the only recorded external parasitoid of *E. ochrogaster*. Cushman (1926), Vance (1927), and Strickland (1923) provided information on the biology of species in this genus. Only a generalized summary of the life history of *Netelia* spp. is given here.

The females deposit one to four stalked eggs on the thoracic region of late instar lepidopterous larvae. Of these only one survives to maturity. Strickland (1923) showed that the egg would remain attached even though the host molted. Cushman (1926) stated that the host larvae were attacked when they were very large and when they were about to pupate in some protective medium. The egg hatches generally after the host has entered a pupation site. The parasitoid larva feeds by puncturing the host integument, attaching its mouthparts, and remaining in one place until new punctures are made necessary. The parasitoid larva remains attached to the egg for most of its life, at least till the final instar. Attachment to the egg shell is accomplished by a special spined area on the terminal abdominal segment. The cast larval skins all remain attached to the egg shell and provide a convenient record of the larval morphology of each instar. The parasitoid develops rapidly and kills the host leaving a dry skin. Shortly after this it spins a cocoon.

As the species which has been reared from cutworms has not been identified, it is not possible to construct a host list. The genus is too large and widespread to be considered in this paper. Townes *et al.* (1961) state that the hosts of *Netelia* are exposed, medium-sized lepidopterous larvae that pupate in the ground. As *Netelia* spp. attack the larvae just before they are to pupate, it is likely that any species is a potential host if it crawls on the soil looking for a pupation site. The examined specimens reared from *E. ochrogaster* were from Saskatoon and Red Deer, Saskatchewan. One empty cocoon which likely was of *Netelia* was found at Calahoo.

Gravenhorstia propinqua (Cresson)

Originally, King and Atkinson (1928) recorded *Erigorgus* sp. as being reared from *E.*

ochrogaster. *Erigorgus* is now considered to be a synonym of *Gravenhorstia* (Townes *et al.*, 1961). Specimens of *Gravenhorstia propinqua* which were reared from *E. ochrogaster* were found in the C.N.C.

Description of cocoon. — The cocoon of this species is spun inside the host pupa. It appears to be lightly constructed of a single layer of silk which likely offers little protection to the parasitoid pupa. The emerging adult destroys the entire anterior end of the host pupa and leaves much of the cocoon visible (Fig. 65). The larval remains are stuck in the posterior end of the cocoon and are easily recovered and handled.

Description of larva. — The cephalic structures of the last larval instar (Fig. 43) are distinct from the other pupal parasitoids and are described as follows: The epistoma is heavy and complete, with superior mandibular processes short, wide and directed ventrally. Inferior mandibular processes are reduced to one which is broad and heavy. Lacinal sclerite is absent. Long, heavy hypostomal arms are curved ventrally in a wide semi-circle so that the ends form a nearly straight line with ends of the labial sclerite. Hypostomal spur absent. Stipital sclerite long, narrow, extending from one-third of way along the hypostoma ventro-medially to a point three-quarters along its length, where it bends sharply dorso-medially to touch the labial sclerite. Labial sclerite incomplete with long narrow arms extending ventrally. Silk press present, very lightly sclerotized forming a wide U-shape. Labral sclerite straight, short and irregular in outline with several vacuoles. Suspensorial sclerite very wide and well developed. Mandibles large, well developed, with distinct blade clearly marked off from base. Maxillary and labial palps clearly distinct. Antennae not observed.

Biology. — Except that it kills the pupal stage of *E. ochrogaster*, little is known of the biology of *Gravenhorstia propinqua*. King and Atkinson (1928) noted that the species they recorded overwintered in the host pupa. One interesting fact appears in the host lists for the genus. Two tortricids have been recorded as hosts, and both larvae were killed by the *Gravenhorstia* sp. In both noctuid hosts, the pupal stage was killed. It is possible that when this genus is studied more carefully, more than one genus will be found within the present concept.

Hosts. — The following hosts have been recorded for *Gravenhorstia* spp.: *Polia purpurissata* Grote (Wood *et al.*, 1954), New Brunswick; *Archips argyrospilus* Walker (Paradis, 1960), Quebec; *Tortrix alleniana* Fern (Martin, 1958), Ontario; *Agrotis orthogonia* (King and Atkinson, 1928). The specimens reared from *E. ochrogaster* were from Saskatchewan.

BRACONIDAE

Morphology of immature braconids

Basically, the methods used to separate the immature stages of ichneumonids apply to those of braconids. In addition, important characters are found in the color, size, shape, and number of cocoons per host in each species. The appearance of the cocoon mass is also of importance.

Four species, *Microplitis kewleyi*, *Apanteles laeviceps*, *A. griffini*, and *A. acronyctae*, from the subfamily Microgastrinae have been recorded as reared from *E. ochrogaster*. Short (1952) stated that the final instar larvae are characterized as follows: hypostoma, stipital sclerite, and labial sclerite present; hypostomal spur reduced; pleurostoma weakly sclerotized; epistoma always absent; antennae not distinct; setae present on body but spines not present. Capek (1970) gives the same basic characters but makes no definite statement about the epistoma. I believe that Short is incorrect in stating that the epistoma is always missing, as it is present in *M. kewleyi*. Capek states that members of the group of genera to which *Apanteles* and *Microplitis* belong are endoparasites of lepidopterous larvae, are often

gregarious, emerge as mature larvae to pupate, and that the emergence hole is regular due to a cap.

Apanteles Foerst

Apanteles acronyctae Riley

Apanteles acronyctae was recorded as being reared from *E. ochrogaster* by King and Atkinson (1928). The record was based on only two specimens reared by the authors. *A. acronyctae* is normally associated only with arctiid hosts and likely does not attack cutworms (Mason, pers. comm.). This record is likely based on a mistaken identification.

Apanteles laeviceps Ashmead

Apanteles laeviceps was recorded as reared from *E. ochrogaster* by Strickland (1923).

Description of cocoon. — The cocoon mass (Fig. 45) contains 22 to 28 individual cocoons. The mass is compact and only rarely was an isolated cocoon observed. The cocoons are tightly woven together and are united in a single irregular deep mass. The individual cocoon (Fig. 46) is 3.0 to 3.2 mm long, cylindrical with bluntly rounded ends, and is lightly constructed. When treated with a mild KOH solution the cocoon structure is completely destroyed. The loose outer layer of silk is tightly interwoven with that of the other cocoons. As with the other braconids, a distinct cap is formed and breaks off when the adult emerges. The color of the mass changes from a pale yellow to white as the cocoons mature. In many cocoons, the contents can be seen through their walls.

Description of larvae. — The penultimate larval stage of *A. laeviceps* (Fig. 47), which is found in the host, differs from the same stage of *Meteorus vulgaris* in the following ways. The cephalic region of *A. laeviceps* is more clearly defined than that of *M. vulgaris*. The body of *A. laeviceps* is long, narrow, and terminated by a bulbous caudal appendage. Overall length is approximately 5 mm, with the widest point measuring 1.8 mm. As in *M. vulgaris*, the larvae molt to the final instar as they escape from the host. The final instar larva was described by Strickland (1923). It differs from that of *M. vulgaris* in that it lacks a definite caudal appendage and has a series of small black spines on its body. It differs from the penultimate stage by not having the globular caudal appendage. In both of the last two larval instars of *A. laeviceps* the mouthparts appear similar. The cephalic structures of the final instar larva with epistoma missing, pleurostoma apparently missing, lower mandibular process blunt and rounded (Fig. 44). Hypostoma heavily sclerotized, long, narrow and curved medially. Hypostomal spur small, distinct, pointed. Stipital sclerite heavily sclerotized, wide with a distinct twist in the mid-area. Labial sclerite complete, well developed, thick at top, narrowed at bottom, sometimes widened at end. Silk press very obscure but large. Maxillary and labial palpi small. Mandibles with long curved blade arising low on mandibular base. Antennae and spiracles not apparent.

Biology. — The females of *A. laeviceps* oviposit in early instar host larvae. This was demonstrated in the current study by rearing early instar cutworms which had been captured in the field, and finding them to be attacked by *A. laeviceps*. The earliest instar cutworm found attacked was an early third instar. The host is usually killed in the fifth or early sixth instar. The larvae of *A. laeviceps* exert a strong influence over the behaviour of the host. Strickland (1923) noted that until the *A. laeviceps* larvae began to attach to the host's cuticle, no ill effects were evident. At this stage, the host leaves the soil and climbs some convenient object such as a grain stem or a large clod of earth. I have observed *E. ochro-*

gaster larvae climbing only when attacked by *A. laeviceps*. While the host is on the object, the parasitoid larvae emerge from all sides of it. The host then crawls away leaving the parasitoids behind. The parasitoids begin to spin their cocoons almost immediately. When studying cutworm outbreaks, cocoon masses of *A. laeviceps* are easily found by examining marker stakes or emergence traps, both of which serve as climbing points for the hosts. The host larva returns to the soil but always dies within a short time. In the laboratory, I have seen *E. ochrogaster* larvae live up to 3 days following *A. laeviceps* emergence. These host larvae are recognizable by the presence of the exuvia-plugged emergence holes of the parasitoid, the presence of one or more *A. laeviceps* larvae in the body cavity which failed to emerge, and by the general lack of damage to the muscles and nerves.

Hosts. — The following hosts have been recorded in the literature: *Eucirrhoidea pampina* Gn. (Wood and Nielson, 1957), New Brunswick; *Spaelotis clandestina* Harrison (Wood, 1951), New Brunswick; *Syngrapha epigaea* Grote (Wood, 1951), New Brunswick; *E. ochrogaster*, *Chorizagrotis auxiliaris* (Strickland, 1923), Alberta; *Meliana albilinea* Hübner (Webster, 1911); *Loxostege sticticalis* L. (Vierick, 1916), *Pseudaletia unipuncta* (Guppy, 1967) Ontario. During the current study *A. laeviceps* was reared from *E. ochrogaster* in 1967 and 1968 and from *Feltia ducens* in 1967.

Apanteles griffini Viereck

Schaffner and Griswold (1934) recorded *Apanteles griffini* as being reared from *E. ochrogaster* in the north-eastern part of the United States.

Description of cocoon. — The cocoon mass of *A. griffini* (Fig. 49) is deeply divided longitudinally so that two distinct but connected portions are evident. The construction and density of the mass is very similar to that of *A. laeviceps*. The groove is likely formed because the larvae pupate almost immediately after emergence and do not move together. The groove corresponds to the location of the host at the time of emergence of the parasitoid larvae.

Description of larvae. — No specimens of the entire larvae were available for study. Cephalic structures of final instar larvae (Fig. 48) similar to those of *A. laeviceps*. Hypostoma less distinctly curved than in *A. laeviceps*. The labial sclerite more narrowly developed than that of *A. laeviceps*. Mandible with a long narrow blade which arises near the center of the base. The base is more triangular than that of *A. laeviceps*. The hypostomal spur is short and bluntly developed.

Biology. — *A. griffini* is generally found in the more southern range of *E. ochrogaster* (Mason, pers. comm.). Little is known of the biology of this species.

Hosts. — Walkden (1950) recorded the following hosts of *A. griffini* from the central great plains, U.S.A.: *Agrotis orthogonia*, *A. gladiaria* Morrison, *Chorizagrotis auxiliaris*, *Peridroma margaritosa* Haworth.

Microplitis kewleyi Muesebeck

Schaffner and Griswold (1934) recorded *Microplitis kewleyi* as being reared from *E. ochrogaster*. Only one specimen was available for study.

Description of cocoon. — The cocoon (Fig. 51) is solitary, small (3.1 x 1.4 mm), has very little outer silk, has a very tough inner layer of silk, and is an opaque buff color.

Description of larvae. — Cephalic structures (Fig. 50) of the final instar larva with a very weakly sclerotized, incomplete epistoma. Superior mandibular process very indistinct, as well as the rest of pleurostoma. Inferior mandibular processes each small and bluntly devel-

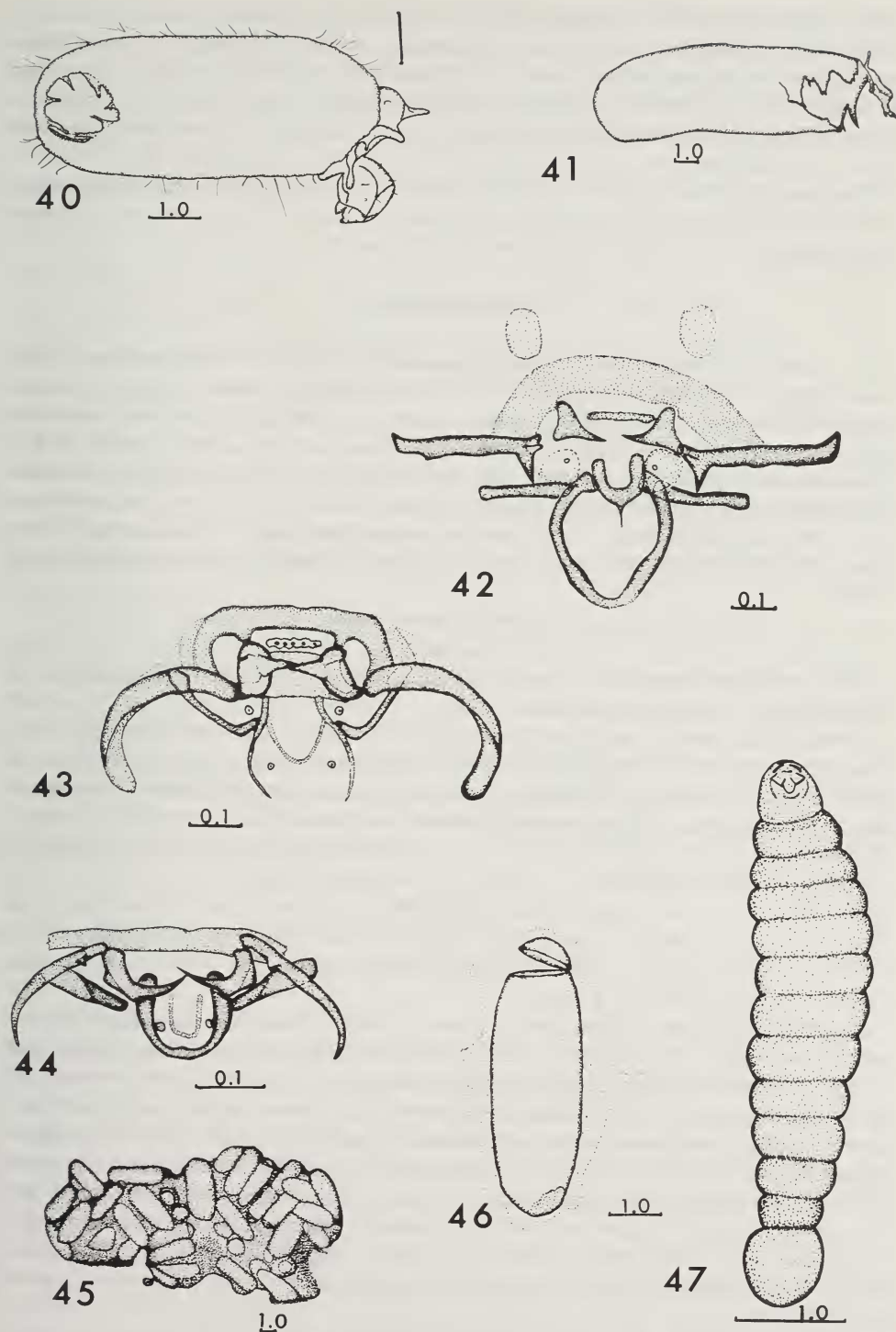


Fig. 40, 42. *Campoletis atkinsoni*. 40. cocoon. 42. cephalic structures of final instar larva. Fig. 41. Cocoon of *Netelia* sp. Fig. 43. *Gravenhorstia propingua* final instar larva cephalic structures. Fig. 44–47. *Apanteles laeviceps*. 44. cephalic structures of final instar larva. 45. cocoon mass. 46. individual cocoon. 47. penultimate larva. Scale in millimeters.

oped. Hypostoma heavily sclerotized, curved medially, with a reduced, pointed hypostomal spur. Stipital sclerite long, narrow, and with irregular outline. Labial sclerite heavily sclerotized, widest at midpoint and narrowed to a point at distal end. Silk press lightly sclerotized, long and narrow. Suspensorial sclerite lightly sclerotized and irregular in form. Mandibles with short narrow blades arising from bottom of mandible bases. The mandible open posteriorly in a distinct groove.

Biology. — Extremely little is known of the biology of this species other than that it attacks larval cutworms. The examined specimen was reared from a cutworm at College Park, Maryland.

Meteorus Haliday

Two species of *Meteorus*, *dimidiatus* Cresson and *vulgaris* Cresson have been recorded as reared from *E. ochrogaster*. Strickland (1923) recorded the former as being a common parasitoid of prairie cutworms. He noted, however, that difficulty had been encountered when the series were identified in distinguishing them from *M. vulgaris*, and Dr. W.R.M. Mason also is sceptical of this record. The current host lists (Graham, 1965) do not include *M. dimidiatus*. All of the *Meteorus* specimens reared from *E. ochrogaster* in my study were *M. vulgaris*. Strickland dealt at length on the biology, hosts, and development of *M. dimidiatus*. This information on the biology of *M. dimidiatus* appears now to be valid for *M. vulgaris*.

Meteorus vulgaris Cresson

This species was recorded as reared from *E. ochrogaster* by King (1926), and has subsequently been recorded several times.

Description of cocoon. — The cocoons are 4.9-5.4 mm x 1.9-2.3 mm, elliptical in shape with the widest point between the posterior one-third and the midpoint (Fig. 55). The anterior end of the cocoon terminates in a distinct cap which breaks off at adult emergence. Specimens which were observed spinning their cocoons formed the cap only after the rest of the cocoon was completed. While the rest of the cocoon turns brown with maturity, the cap remains a much lighter color. The cocoons are usually translucent so that the contents are easily seen. An outer layer of fine silk binds the cocoon to the substrate and to surrounding cocoons. The cocoon mass (Fig. 54) is very loose and irregular, and it is common to find cocoons completely separated from the rest of the mass. The larval remains are easily found and removed from the cocoons.

Description of larvae. — Cephalic structures of the final instar (Fig. 52) with incomplete, lightly sclerotized epistoma. Each superior mandibular process well developed, inferior mandibular processes small and blunt, lacinial sclerite small and pointed. Hypostomal arms short, narrow curved, and only lightly sclerotized. Pleurostoma distinctly sclerotized as opposed to light sclerotization of the epistoma and hypostoma. Stipital sclerite long, narrow, almost straight, reaching upper end of labial sclerite. Labial sclerite large, heavy and greatly thickened in ventral portion. Silk press well developed and moderately sclerotized. Well-developed pharyngeal region with lightly sclerotized ridges behind silk press and top of labial sclerite. Mandibles small, with short, pointed, conical blades well set off from base. Maxillary palps large and with well-developed membranous projection. Antennae large and well developed.

Strickland provided figures of the entire final instar larva and of the penultimate larva. The larva normally molts as it emerges from the host leaving the exuvia of penultimate larva in the emergence hole. The penultimate larva as shown by Strickland has a long caudal

appendage whereas the final instar larva has a much reduced caudal appendage. No larvae similar to that described by Strickland as the penultimate instar were found during my study. The shape of the final instar larva (Fig. 53) changes as the cocoon is spun. The larva shortens and thickens, the segmentation becomes less defined, and the caudal appendage becomes more obscure. When dissecting host specimens from which *M. vulgaris* larvae had emerged, it was found that one to three larvae were usually remaining in the host. These appeared the same as the final instar larvae and likely molted even though they failed to emerge.

Biology. — The biology of the immature stages of *M. vulgaris* is well documented by Strickland (1923). Normally, 24 to 28 pupae were reared from a single host but as many as 36 were reached during my study. The hosts killed by *M. vulgaris* during 1967 and 1968 were in the late stages of the sixth instar. In most cases, the host larva crawled away from the *M. vulgaris* pupae and died. Dissection of the host cutworm after the emergence of the *M. vulgaris* larvae revealed that the muscle layers were partially destroyed, as is the case with other parasitoids. The exuviae of the penultimate instar larvae formed blackened areas on the cutworm integument indicating the emergence points. These usually occur on the ventro-lateral portion of the cutworm's body. The presence of the cast exuviae gives the cutworm a characteristic appearance, aiding in recognition of the cutworm after the *M. vulgaris* larvae have emerged, but before the death of the host. In two cases, *M. vulgaris* pupal masses were found in the loose upper soil. The adults emerge from the pupae 14 to 17 days after pupation.

Hosts. — The following hosts have been recorded for *M. vulgaris*: *Euxoa ochrogaster* (King and Atkinson, 1928; King, 1926) Saskatchewan; *E. tristicula* (King, 1926) Saskatchewan; *Peridroma saucia* (Fletcher, 1901); *Syngrapha epigaea* (Wook and Nielson, 1960) New Brunswick. Strickland (1923) reared *M. vulgaris* (or *dimidiatus*) from the following hosts captured in Alberta: *A. orthogonia*, *E. ochrogaster*, *C. auxiliaris*, *E. tristicula*, *S. devastator* Brace, *Actebia fennica*. Walkden (1950) listed the following hosts of *M. vulgaris* from the central great plains, U.S.A.: *A. orthogonia*, *A. gladiaria*, *A. ypsilon*, *C. auxiliaris*, *Feltia subgothica* Haworth, *Euxoa messoria*, *Peridroma margaritosa*. I reared *M. vulgaris* from *Feltia ducens* in the summer of 1967.

ENCYRTIDAE

Copidosoma bakeri (Howard)

Copidosoma bakeri is probably the most important single parasitoid of *E. ochrogaster* over most of its range. This species was first described in the genus *Berecyntus* and most of the literature associated with this species is found under *Berecyntus bakeri*. Originally *C. bakeri* was described as a single species with several varieties including *gemma* Girault, *arizonensis* Girault, *euxoae* Strickland, and *bakeri* Girault. Other workers gave these varieties subspecific rank (Gibson, 1917; Peck, 1951). Peck (1963) states that *C. bakeri* cannot be subdivided into varieties or subspecies, as the earlier groupings are merely a reflection of color patterns and not of population differences.

Biology. — Work on the biology and development of *C. bakeri* has been published by Gibson, 1915; Strickland, 1916; King and Atkinson, 1928; and Cook, 1930. The most extensive work done on this species was that of McMillan (1930) in an unpublished masters thesis.

C. bakeri oviposits in the eggs of its many hosts but the host is not killed until the approximate time that host pupation occurs. The polyembryonic development of *C. bakeri*

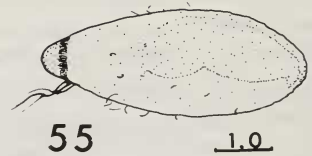
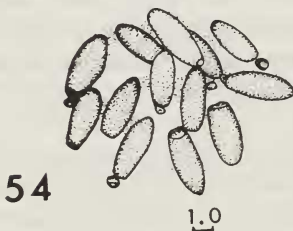
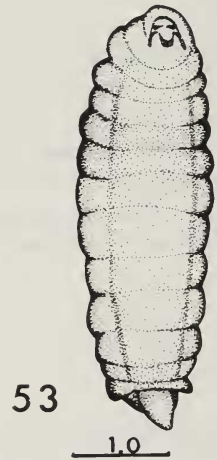
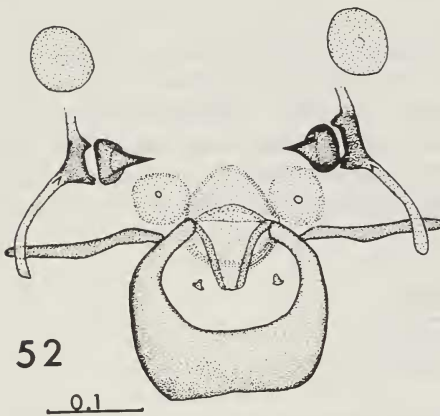
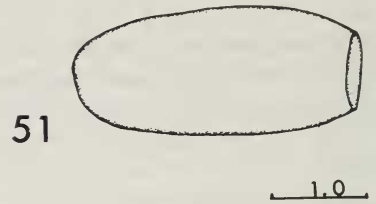
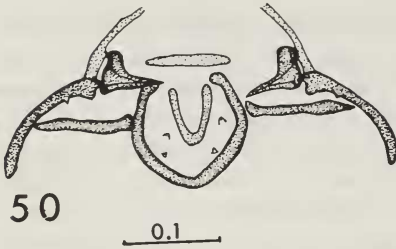
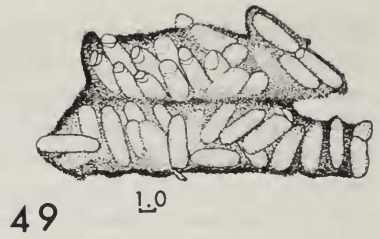
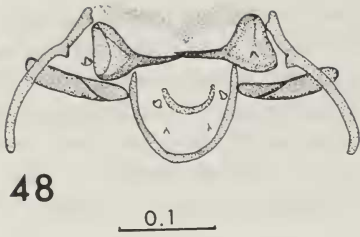


Fig. 48, 49. *Apanteles griffini*. 48. cephalic structures of final instar larva. 49. cocoon mass. Fig. 50, 51. *Microplitis kewleyi*. 50. cephalic structures of final instar larva. 51. cocoon. Fig. 52–55. *Meteorus vulgaris*. 52. cephalic structures of final instar larva. 53. final instar larva. 54. cocoon mass. 55. cocoon. Scale in millimeters.

will be discussed later.

McMillan (1930) observed *C. bakeri* adults in the field in central Saskatchewan from early May until the end of August, while I observed them during the latter portion of July and most of August. The great length of time during which adults occur in the field is due to the emergence from different host species completing development at different times during the summer. *C. bakeri* adults emerge from *E. ochrogaster* larvae at approximately the same time as do the *E. ochrogaster* adults. In the laboratory the maximum time which *C. bakeri* adult females can be kept alive is 16 days, with a mean of 11 days (McMillan, 1930). It is likely that eggs of *E. ochrogaster* are exposed to only a small portion of the *C. bakeri* adults which emerged from *E. ochrogaster* larvae because of the long preoviposition period of *E. ochrogaster* females. A detailed biology of adult *C. bakeri* may be found in McMillan (1930).

The parasitic egg develops for approximately 45 days within the host egg till it reaches an overwintering stage. During this time it has approximately doubled in size and is transformed into a syncytium of cleavage nuclei surrounded by a trophamnion (McMillan, 1930). The trophamnion provides nutriment for the embryonic mass from the host tissues as the eggs of polyembryonic parasitoids are relatively free of yolk (Chapman, 1969). After the host emerges from its egg, the growth of the polyembryonic mass resumes. The actual mechanism of polyembryonic development is described by McMillan (1930) and Leiby (1922).

The earliest that a polyembryonic body (p.e.b.) was detected in my dissections of red-backed cutworms was in the third instar of the host. The polyembryonic body at this time is very small, compact and is usually flattened and little internal differentiation is apparent. It grows in size in the next instars of the host until it fills a major portion of the area between the gut and the muscle layer under the integument. At this point it may be present as a simple flattened structure or it may be lobed or divided into smaller bodies. If more than one p.e.b. is present in the host then one is usually much more developed than the other. There were never two distinct p.e.b.'s in the same area of the host's body. The body remains largely undifferentiated until either the sixth or seventh instar of the host, depending upon whether an extra instar occurs. The p.e.b. then begins to divide into smaller embryonic units which are marked by density changes in the p.e.b. These embryonic units change to spherical structures and give the entire p.e.b. the appearance of a bag of marbles. These structures change into the form of larvae while still in the intact p.e.b. The p.e.b. in the meantime becomes larger and more deformed till it is very lobed. When the larvae are fully developed within the body, they begin to escape from it. Several dissections were made at the time when the p.e.b. had begun to disintegrate and the larvae spread throughout the host body. Not all the larvae appeared to leave the p.e.b. simultaneously; in fact, some of the remaining larvae were less developed and likely did not complete their development before the earlier-developing larvae destroyed both the host and the remains of the p.e.b. Occasionally, some larvae were found free of the p.e.b. before the majority of the larvae were mature enough to leave the p.e.b. These likely correspond to the pseudolarvae referred to by Leiby (1922, 1926). The pseudolarvae are actually larvae which failed to obtain sufficient nutrition while in the p.e.b., and will not survive to the pupal stage.

Once the larvae break free of the p.e.b., they begin to actively ingest the host body contents. This is a very rapid process taking 2 to 4 days.

The behaviour of the host changes radically during the last stages of intact p.e.b. and the beginning of the parasitoid larval attack. The host eats more during the last period than does the normal cutworm (McMillan, 1930). As the p.e.b. breaks down the host is very active and restless. Strong turning and twisting activity is often noticed. Feeding ceases during this period. The parasitoid larvae distribute themselves throughout the body and rapidly

destroy the internal organs leaving the external musculature and nerve network until last. The host is usually capable of reflexes i.e. curling movements even if the entire internal structure is destroyed. Finally, the muscles, brain, and nervous system are eaten leaving only a 'plastic' bag of host integument full of parasitoid larvae. In one case, even this integument bag was destroyed. The external appearance also changes radically from the attack of the larvae. Sometimes the intact p.e.b. can be seen through the intersegmental membranes of the host as a solid white mass which does not move like the surrounding fat body. The host at this stage is a typical dorsal red and ventral clear light grey. The crawling and curling movements appear normal. As the p.e.b. begins to break down, the color of the body changes. The reds become lighter and pass through a pale pink and then become an off-grey. The ventral surface changes from the clear grey to a mottled grey as the parasitoid larvae can be seen through the integument (Fig. 59). As the last muscle and nerve tissue is destroyed, a fluid discharge is emitted from the body of the host which leaves a brown stain on the filter paper of a culture dish. The host is now a uniform buff-grey shade and the larvae are packed into every portion of the body including the prolegs, brain and eyes (Fig. 58). The body of the host sags to the most stable shape, which in culture dishes fits the pattern of the objects on which it lies. Specimens found in the field were flattened, screw-shaped, or almost normally curved. The *C. bakeri* larvae pupate within 2 days of the host body collapse.

As the pupae mature, the color of the host carcass darkened noticeably due to the color change of the individual pupae. After 14 to 26 days the adults emerge in a period of 6 to 12 hours. The host carcass is perforated with holes on all sides except the bottom. Each adult does not form a new hole but will use an old hole if one exists near it. After emergence the host resumes a dull grey or tan color.

The individual larvae (Fig. 56) of *C. bakeri* have very few distinctive characters. McMillan (1930) gives a figure of the mandibles of the larvae, but I found the mandibles so hard to obtain and study that I regard them as being essentially useless as an identifying character. *C. bakeri* larvae are easily distinguished from other larvae likely to be found attacking *E. ochrogaster* by their great numbers and by their lack of sclerotized characters. Late larvae or prepupae (Fig. 57) are also easily recognized as the host is essentially destroyed by the time of their appearance.

Hosts. — *C. bakeri* has a wide range of natural hosts. The following hosts were recorded by Peck (1963) with the authors he cited and additional references. Location by province or state is included to provide additional information on the distribution of both the host and the parasitoid: a. *Agrotis orthogonia* (Cook, 1930), Montana; b. *A. venerabilis* Walker (King and Atkinson, 1928), Saskatchewan; c. *Amathes smithi* Snellen (Wood and Nielson, 1957), New Brunswick; d. *Chorizagrotis auxiliaris* (Strickland, 1916; Girault, 1917), Alberta; (Snow, 1925), Utah; (Walkden, 1950), Kansas; e. *C. thanatologia* (King and Atkinson, 1928), Saskatchewan; f. *Chorizagrotis* sp. Sm. (Girault, 1916), Arizona; g. *Crymodes devastator* (Gibson, 1915, 1917; Girault, 1916; Treherne, 1915), Ontario; h. *Euxoa detersa* Walker (King and Atkinson, 1928), Saskatchewan; i. *E. flavicollis* (King and Atkinson, 1928), Saskatchewan; j. *E. intrita* Morrison (Cook, 1930), Montana; k. *E. messoria* (Walkden, 1950), Kansas; l. *E. ochrogaster* (King and Atkinson, 1928), Saskatchewan; m. *E. scandens* (Walkden, 1950), Kansas; n. *E. tristicula* (Strickland, 1921; Whitehouse, 1922), Alberta; (King and Atkinson, 1928), Saskatchewan; o. *Euxoa* sp. (Girault, 1916; Gibson, 1917), Ontario; p. *Feltia ducens* (King and Atkinson, 1928), Saskatchewan; q. *Feltia subgothica* (Walkden, 1943, 1950), Kansas; (Peck, 1951), Kansas, Alberta, New Mexico; r. *Lacinopolia renigera* Stephens (Walkden, 1950), Kansas, s. *Pissodes strobi* (Taylor, 1929), Massachusetts.

McMillan's (1930) thesis lists nine of the above species as hosts of *C. bakeri*. In addition

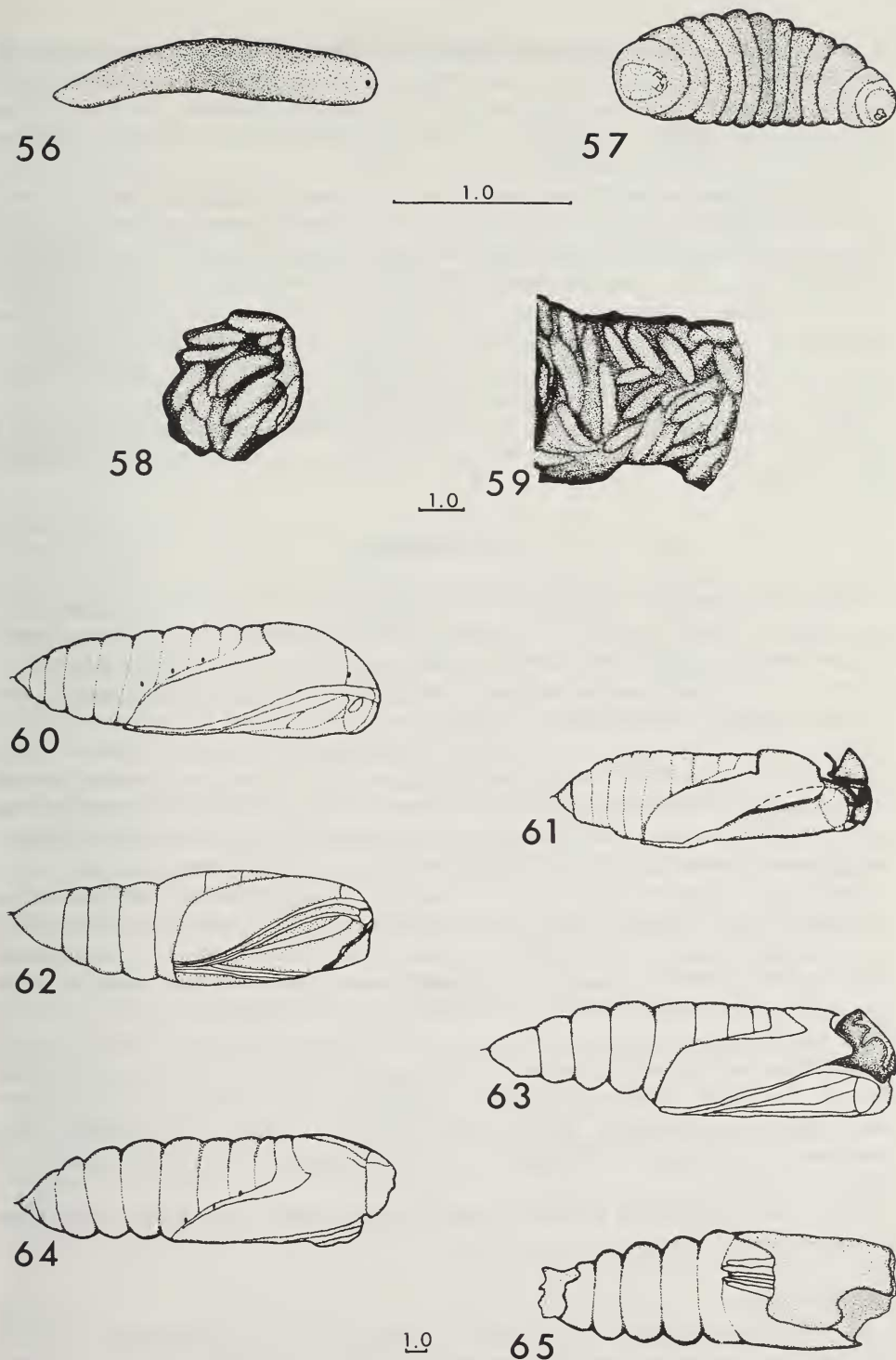


Fig. 56–59. *Copidosoma bakeri*. 56, feeding larva. 57, prepupa. 58, cross-section of host at completion of *C. bakeri* feeding. 59, surface view of above. Fig. 60–65. *E. ochrogaster* pupae. 60, normal before moth emergence. 61, normal after moth emergence. 62, after *Gonia* spp. emergence. 63, after *Poecilanthrax alcyon* emergence. 64, after ichneumonine emergence. 65, after *Gravenhorstia propingua* emergence. Scale in millimeters.

six more species are given in which parasitism was induced. They are *Euxoa tessellata*, *E. verticalis* Grote, *E. dargo* Stkr., *E. divergens* Walker, *E. campestris* Grote, *L. renigera*. McMillan felt that natural parasitism does not occur in these species because they normally lay their eggs in hard packed prairie soil. He proved that firmly packed soil provides an effective barrier to *C. bakeri* oviposition.

Of the 20 species which I have listed as recorded hosts, I believe that one is in error. The species *Pissodes strobi*, the white pine weevil, attacks the shoots of white pine trees. (*Pinus strobus*). The list from which Peck (1963) derived his information is headed 'Parasites reared from *P. strobi* or weeviled material' (Taylor, 1929) and is data from several different workers. All other recorded hosts are cutworms which are typically found in open areas and whose eggs are laid on or near the soil, while *P. strobi* is a weevil and occurs in wooded areas. Also, *P. strobi* lays its eggs in the tips of white pine shoots so that it is very unlikely that one parasitoid would attack such a wide range of hosts in such divergent habitats.

During the present study *C. bakeri* was reared from *Feltia ducens* during the summer of 1967, and from *E. ochrogaster* in 1967 and 1968 and was dissected from *E. ochrogaster* larvae in 1969.

DISCUSSION

Twenty-seven species of parasitoids have been recorded as reared from *Euxoa ochrogaster*. Three of these records, *Gonia capitata*, *Apanteles acronyctae*, and *Meteorus dimidiatus* are incorrect. Of the 24 species of confirmed parasitoids, the immature stages of 15 are described. Of the remaining species, Brooks (1952) has provided descriptions of four of the bombyliids. *Pseudamblyteles subfuscus* and *Gonia* sp. were not described as I was not able to find what species these records are now valid for and thus could not locate specimens. *Gonia fuscicollis*, *Villa lateralis*, and *Agamermis* sp. were not described because I could obtain no specimens of any of the immature stages. Because of the possibility that both *Periscepsia laevigata* and *Gonia sequax* are parasitoids of the red-backed cutworm, descriptions of the available immature stages of these species have been included.

The known biology of each species of parasitoid is given in the text and some of this information is summarized in Table 1. It should be noted that the stage of the host in which the parasitoid lays its egg was determined either by literature records or by using rearing data from field-collected specimens. The earliest instars selected by the parasitoid can be calculated by determining both the instar and the time of the season in which the host, which later produced a parasitoid, was captured. The latest instars can be found by dissections of host material and sometimes by observing the oviposition behaviour of the parasitoid. For example, no specimens of the red-backed cutworm collected before the fourth instar produced ichneumonine adults. When sixth instar cutworms were attacked in the laboratory, the ichneumonine females were unable to lay eggs in the host because of its defense reactions.

Figure 66 summarizes the parasitoid complex and the stages at which the parasitoid eggs are laid and those at which the hosts are killed.

Alternative hosts

All the better known species of parasitoids in this study have several hosts from which they have been reared and recorded. Indubitably, for each of these species of parasitoids, there are more hosts which have yet to be recorded. Most host records for parasitoids result from the rearing of economic species, and there is little reason to suspect that these parasitoids attack only hosts which are of economic importance. With the exception of *Villa*

Table 1. Summary of the biology of *E. ochrogaster* parasitoids.

| Species | Status | Stage attacked | Stage killed | No. of known hosts |
|----------------------------------|------------------|----------------|--------------|--------------------|
| Tachinidae | | | | |
| <i>Gonia aldrichi</i> | confirmed | IV, V, VI | pupa | 2 |
| <i>Gonia capitata</i> | rejected | — | — | — |
| <i>Gonia fuscicollis</i> | confirmed | IV, V, VI | pupa | 1 |
| <i>Gonia sequax</i> | suspected | IV, V, VI | pupa | 1 |
| <i>Bonnetia comta</i> | confirmed | III, IV | prepupa | 7 |
| <i>Periscepsia helymus</i> | confirmed | larva | VI | 17 |
| <i>Periscepsia laevigata</i> | suspected | larva | V | 5 |
| Bombyliidae | | | | |
| <i>Villa alternata</i> | confirmed | IV, V, VI | pupa | 6 |
| <i>Villa fulviana</i> | confirmed | IV, V, VI | pupa | 1 |
| <i>Villa lateralis</i> | confirmed | IV, V, VI | pupa | 1 |
| <i>Villa moroides</i> | hyper parasitoid | — | — | — |
| <i>Poecilanthrax alcyon</i> | confirmed | IV, V, VI | pupa | 5 |
| <i>Poecilanthrax willistonii</i> | confirmed | IV, V, VI | pupa | 9 |
| Ichneumonidae | | | | |
| <i>Eutanyacra suturalis</i> | confirmed | IV, V, ?VI | pupa | 4 |
| <i>Diphyus</i> No. 1 | confirmed | IV, V, ?VI | pupa | 3 |
| <i>Spilichneumon superbus</i> | confirmed | IV, V, ?VI | pupa | 6 |
| <i>Pseudamblyteles subfuscus</i> | ? | — | — | — |
| <i>Compoletis atkinsoni</i> | confirmed | I, II | III, IV | 1 |
| <i>Netelia</i> sp. | confirmed | V, VI | prepupa | — |
| <i>Gravenhorstia propingua</i> | confirmed | larva | pupa | 1 |
| Braconidae | | | | |
| <i>Apanteles acronyctae</i> | rejected | — | — | — |
| <i>Apanteles laeviceps</i> | confirmed | II, III | V | 8 |
| <i>Apanteles griffini</i> | confirmed | ?II, III | ?V | 4 |
| <i>Microplitis kewleyi</i> | confirmed | ?III, IV | ?IV, V | 1 |
| <i>Meteorus vulgaris</i> | confirmed | III, IV | VI | 14 |
| <i>Meteorus dimidiatus</i> | rejected | — | — | — |
| Encyrtidae | | | | |
| <i>Copidosoma bakeri</i> | confirmed | egg | VI or VII | 19 |
| Nematoda Merinithidae | | | | |
| <i>Agamerimis</i> sp. | confirmed | ? | — | — |

alternata, all parasitoids recorded as reared from *E. ochrogaster* were mainly restricted to noctuid larvae as additional hosts. I believe it is necessary to consider the type of habitat in which all of the species in this host-parasitoid complex existed before agricultural practices modified large areas. Large numbers of cutworm species probably existed in low densities in the prairie and parkland areas of Canada. The densities of individual host species were probably low enough to prevent host-parasitoid complexes restricted to small numbers of species from occurring. In order to survive, each parasitoid species probably had to attack any host in a given taxonomic range in a given habitat type. The hosts of some of the species include ground cutworms and climbing cutworms which are found in grasslands, fields or low bush open areas.

Cutworms such as *E. ochrogaster* were probably adapted to feeding in areas of recently disturbed soil. This is reflected by the preference of the female to lay her eggs in loose soil. One of the parasitoids, *Copidosoma bakeri*, is also restricted to areas of loose soil. McMillan (1930) showed that *C. bakeri* was capable of completing development in species normally found only in packed soil but that in the field they are unable to penetrate the soil and find the eggs. It is likely that the high degree of polyembryony in *C. bakeri* is the result of the unstable nature of the habitat it requires and the relative difficulty of finding such a habitat. As agriculture has increased the amount of disturbed soil and at the same time made the cutworm habitat more stable, the densities of both the host species and their parasitoids have probably increased.

Regulation of *E. ochrogaster* populations by parasitoids

Nine species of parasitoids were reared from *E. ochrogaster* during this study. The estimated percentages of hosts killed in the 1967 and 1968 seasons are given in Table 2. These estimates were calculated using the number of hosts killed by a parasitoid (or which contained immature stages of that parasitoid) out of the total number of hosts entering the stage which the parasitoid normally killed. As was found by King and Atkinson (1928), *Gonia aldrichi*, *Meteorus vulgaris*, *Campoletis atkinsoni*, and *Copidosoma bakeri* were important parasitoids. Interestingly, King and Atkinson found no ichneumonine species as parasitoids of *E. ochrogaster*, while I found three. Of these, *Spilichneumon superbus* was the most important species and *Diphyus* No. 1 may be important in other years. The total ichneumonine complex is an important regulatory factor in the population fluctuations of the red-backed cutworm. *A. laeviceps* was recorded by Strickland (1923) as killing 5% of the red-backed cutworms in 1915 and less than 1% in 1916. In 1967, the number of fifth instar larvae collected was too low to permit estimation of the mortality caused by *A. laeviceps*. In 1968, only one collected red-backed cutworm was killed by *A. laeviceps*. It does not appear as if this species was important in regulating the numbers of *E. ochrogaster* during 1967 and 1968.

It appears from my study and from the work of King and Atkinson (1928), that the parasitoids are not the chief controlling factors of *E. ochrogaster* populations, but are important regulating factors.

Figure 67 shows the decrease in size of the *E. ochrogaster* population at Calahoo in the summer of 1968. The population estimates were made weekly and were based on 20 one-half square meter samples. These samples were taken using a modified random sampling plan within a 100 quadrat sampling area. The sampling area was 100 meters square. The soil was removed to a depth of 15 cm and sieved using a mechanical shaker.

The decrease shown is far more rapid than if parasitoids were the most important regulating factors. Frank (1971a) does not feel that carabid predators are the controlling factor either. It is likely that the reduction of population is due to a complex interaction of

predators, diseases, and parasitoids. All of these factors are likely directly influenced by the weather conditions within any season. Until more intensive research is carried out on the total regulatory complex, the most important controlling factor must remain in doubt.

Table 2. The estimated mortality caused by the species of parasitoids reared from *E. ochrogaster* at Calahoo in 1967 and 1968.

| Species | 1967 | 1968 |
|-------------------------------|---------|------|
| <i>Gonia aldrichi</i> | 5 - 10% | 9% |
| <i>Eutanyacra suturalis</i> | < 5% | 3% |
| <i>Diphyus</i> No. 1 | < 5% | 5% |
| <i>Spilichneumon superbus</i> | 5 - 10% | 10% |
| <i>Campoletis atkinsoni</i> | — | 9% |
| <i>Apanteles laeviceps</i> | ≅ 5% | < 1% |
| <i>Meteorus vulgaris</i> | 10% | 5% |
| <i>Copidosoma bakeri</i> | 35% | 22% |
| <i>Agamermis</i> sp. | < 1% | 0 |

Economic benefits of parasitoids

In addition to analyzing the effect of any parasitoid on the yearly population fluctuations of *E. ochrogaster* the influence of this parasitoid on the amount of damage caused in any given year must be considered. To reduce the damage done, feeding by the cutworms must be reduced or prevented. Because it kills the early instar larvae *Campoletis atkinsoni* essentially prevents economic damage, and its rate of killing hosts is its rate of economic return. *Apanteles laeviceps*, which kills during the host's fifth instar, reduces the damage done by the hosts which it attacks. *A. laeviceps* has shown a very low rate of attack during my study. While *C. atkinsoni* and *A. laeviceps* reduce the loss caused by their hosts, *Copidosoma bakeri* increases the loss by the current generation. McMillan (1930) found that hosts attacked by *C. bakeri* consumed 27.5% more food than did normal hosts. If a seventh instar occurs, this extends the feeding period of each host. As *C. bakeri* attacks at a fairly high rate, the increased loss due to its presence probably exceeds that prevented by *C. atkinsoni* and *A. laeviceps*. The other parasitoids kill at such low rates, or kill after the host damage has occurred and appear to be economically neutral i.e. they neither increase nor decrease the loss during that season.

Future research

My approach has been to study each of the known parasitoids of *E. ochrogaster* and its geographic range. The knowledge of the parasitoid complex is a reflection of the area where this host is most commonly a pest, namely western Canada. It appears that *E. ochrogaster*, or in fact any economic cutworm, is attacked by the normal parasitoid complex which attack cutworms. The parasitoid complex of any given host could change or be very different in different regions. I believe that it is very difficult at this point to study all the parasitoids of any host which covers a wide geographic range. A more valuable approach may be to

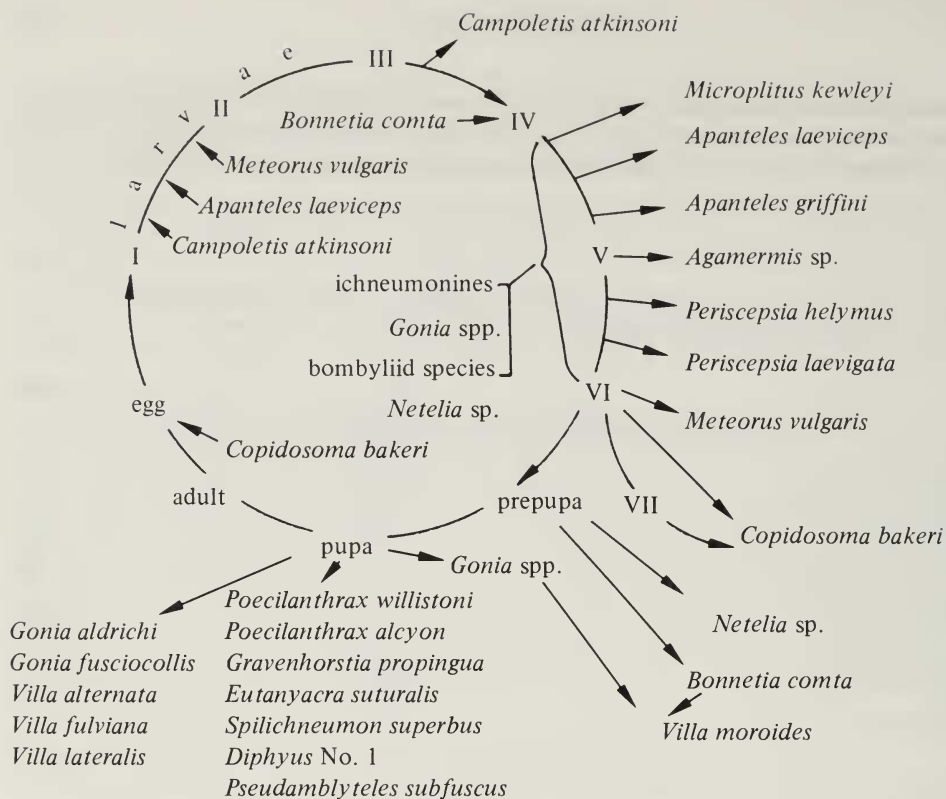


Fig. 66. The parasitoid complex of *Euxoa ochrogaster*. Arrows entering the circle indicate oviposition by the parasitoids. Arrows leaving the circle indicate the stage at which the host is killed.

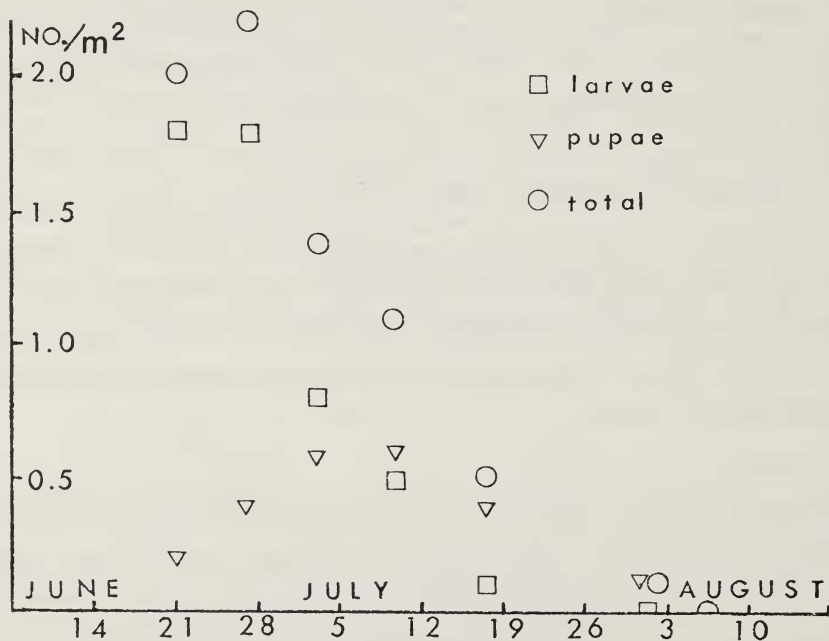


Fig. 67. The decline of the *Euxoa ochrogaster* population at Calahoo, Alberta in the summer of 1968.

study the complex of hosts and parasitoids in any given region. In such a study, all of the parasitoids of all the cutworm hosts which are found in that region would be studied and described. As a result of such a study, all the potential parasitoids of any cutworm species found within that region would be known. The advantages of such an approach are that when any one species is studied some of its actual parasitoids may not be present in sampled populations. If several species of hosts are studied than any one parasitoid is less likely to be overlooked and thus will be recognized in a future outbreak of cutworms. Also, if a different species of cutworm appears in a region, most of the potential parasitoids will be easily recognized, allowing a meaningful analysis of the role of the parasitoids as regulation factors.

ACKNOWLEDGEMENTS

I would like to acknowledge the help which W. G. Evans, my supervisor, provided during this study. I would also like to thank J. H. Frank for his valuable help and advice. Also, I would like to thank M. Wook, F. J. McAlpine, O. Peck, and W. R. Mason of the Canadian National Collection for their help and advice. This study was supported in part by a grant (No. AR 67-31) from The Alberta Agriculture Research Trust.

REFERENCES

- Allen, H. W. 1921. Notes on a bombyliid parasite and a polyhedral disease of the southern grassworm, *Laphygma frugiperda*. J. econ. Ent. 14:510-511.
- Allen, H. W. 1926. Observations upon the early maggot stage of *Linnaemyia comta* Fall, (Diptera Tachinidae). Ent. News 37:283-286.
- Baker, A. W. 1914. The army worm in Ontario in 1914. Rep. ent. Soc. Ont. 45:75-90.
- Berg, V. L. 1940. The external morphology of the immature stages of the bee fly, *Systoechus vulgaris* Loew, (Diptera, Bombyliidae), a predator of grasshopper egg pods. Can. Ent. 72:169-178.
- Bohart, G. E., W. P. Stephen and R. K. Eppley. 1960. The biology of *Heterostylum robustum* (Diptera, Bombyliidae), a parasite of the alkali bee. Ann. ent. Soc. Am. 53(3):425-535.
- Brooks, A. R. 1943. A review of the North American species of *Gonia sens. lat.* Can. Ent. 75:219-236.
- Brooks, A. R. 1952. Identification of bombyliid parasites and hyperparasites of Phalaenidae of the prairie provinces of Canada, with descriptions of six other bombyliid pupae (Diptera). Can. Ent. 84:357-373.
- Capek, M. 1970. A new classification of the Braconidae (Hymenoptera) based on the cephalic structures of the final-instar larva and biological evidence. Can. Ent. 102:846-875.
- Chapman, R. F. 1969. The insects—structure and function. Elsevier, New York, 819 pp.
- Clausen, C. P. 1928. *Hyperalonia oenomaus* Rond., a parasite of *Tiphia* larvae (Dip., Bombyliidae). Ann. ent. Soc. Am. 21:642-658.
- Clausen, C. P. 1940. Entomophagous Insects. McGraw-Hill Book Co. Inc., New York, 688 pp.
- Cook, W. C. 1930. Field studies of the pale western cutworm (*Porosagrotis orthogonia* Morr.) Bull. Mont. agri. Exp. Stn. 225:30-31.
- Cushman, R. A. 1926. Some types of parasitism among the Ichneumonidae. Proc. ent. Soc. Wash. 28:25-62.
- Doutt, R. L. Biological characteristics of entomophagous adults. Chapter 6, Section 3. In De Bach, P. (ed.) Biological control of insect pests and weeds. Chapman and Hall, Ltd. London, 844 pp.

- Finlayson, Thelma. 1960. Taxonomy of cocoons and puparia, and their contents, of Canadian parasites of *Neodiprion sertifer* (Geoff.) (Hymenoptera: Diprionidae). Can. Ent. 92:20-47.
- Fletcher, J. 1901. Report of the entomologist and botanist. 1900, Canada. Central Experimental Farm Ann. Report of the Director, 1900; 195-249.
- Frank, J. H. 1971a. Carabidae (Coleoptera) as predators of the red-backed cutworm in central Alberta. Can. Ent. 103:1039-1044.
- Frank, J. H. 1971b. Carabidae (Coleoptera) of an arable field in Central Alberta. Quaest. ent. 7:237-252.
- Gibson, A. 1915. Cutworms and their control. Dominion of Canada Dept. of Agric., Entomology Branch, Ottawa, Bull. no. 10, 1915. 31 pp.
- Gibson, A. 1917. The entomological record. Rep. ent. Soc. Ont. 47:137-171.
- Girault, A. A. 1916. New Encyrtidae from North America. Psyche Camb. 23:41-50.
- Girault, A. A. 1917. Descriptions Stellarum Novarum. No publisher. 22 p.
- Graham, A. R. 1965. A preliminary list of the natural enemies of Canadian agricultural pests. Information Bulletin No. 4, Research Institute, Canada Department of Agriculture, Belleville, Ontario.
- Greene, C. T. 1921. An illustrated synopsis of the puparia of 100 muscoid flies. Proc. U. S. natn. Mus. 60:1-39.
- Guppy, J. C. 1967. Insect parasites of the armyworm, *Pseudaletia unipuncta* (Lepidoptera: Noctuidae), with notes on species observed in Ontario. Can. Ent. 99:94-106.
- Hardwick, D. F. 1965. The *ochrogaster* group of the genus *Euxoa* (Lepidoptera: Noctuidae), with description of a new species. Can. Ent. 97:673-678.
- Heinrich, G. H. 1960. Synopsis of Nearctic Ichneumoninae Stenopneusticae with particular reference to the northeastern region (Hymenoptera). Part II pp. 91-205. Synopsis of the Ichneumonini: Genera *Orgichneumon*, *Cratichneumon*, *Homotherus*, *Aculichneumon*, *Spilichneumon*. Can. Ent. 92: Supplement 18.
- Heinrich, G. H. 1961. Synopsis of Nearctic Ichneumoninae Stenopneusticae with particular reference to the northeastern region (Hymenoptera). Part IV. pp. 371-505. Synopsis of the Ichneumonini: Genera *Chasmias*, *Neamblymorpha*, *Anisopygys*, *Limerodops*, *Eupalamus*, *Tricholabus*, *Pseudamblyteles*, *Eutanyacra*, *Ctenichneumon*, *Exephanes*, *Ectopimorpha*, *Pseudoamblyteles*. Can. Ent. Supplement 23.
- Hynes, H. B. N. 1947. Observations on *Systoechus somali* (Diptera, Bombyliidae) attacking the eggs of the desert locust (*Schistocera gregaria* Forskal) in Somalia. Proc. R. ent. Soc. Lond. Series A 22:79-85.
- Jacobson, L. A. 1970. Laboratory ecology of the redbacked cutworm, *Euxoa ochrogaster* (Lepidoptera: Noctuidae). Can. Ent. 102:85-89.
- King, K. M. 1926. The red-backed cutworm and its control in the prairie provinces. Can. Dep. Agric. Pamphlet No. 69 new series.
- King, K. M., and N. J. Atkinson. 1928. The biological control factors of the immature stages of *Euxoa ochrogaster* Gn. (Lepidoptera, Phalaenidae) in Saskatchewan. Ann. ent. Soc. Am. 21:167-188.
- Leiby, R. W. 1922. The polyembryonic development of *Copidosoma gelechiae*, with notes on its biology. J. Morph. 37(1):195-285.
- Leiby, R. W. 1926. The origin of mixed broods in polyembryonic Hymenoptera. Ann. ent. Soc. Am. 19:290-299.
- Martin, J. L. 1958. Observations on the biology of certain tortricids in young coniferous plantations in southern Ontario. Can. Ent. 90:44-53.
- McMillan, E. 1930. A preliminary study of the polyembryonic cutworm parasite *Berecynthus*

- bakeri* var. *gemma* Girault. Unpublished masters thesis, University of Saskatchewan.
- Menees, J. H. 1962. The skeletal elements of the gnathocephalon and its appendages in the larvae of the higher Diptera. *Ann. ent. Soc. Am.* 55:607-616.
- Morrison, F. O. 1940. A revision of the American species of *Gonia* Meigen (Diptera: Tachinidae). *Can. J. Res.* 18:336-362.
- Painter, R. H. and J. C. Hall. 1960. A monograph of the genus *Poecilanthrax* (Diptera, Bombyliidae). *Kans. Agric. Expt. Sta. Tech. Bull.* 106:5-132.
- Paradis, R. O. 1960. Essai d'analyse des facteurs de mortalité chez *Archips argyrospilus* (Wlk.) (Lepidoptères: Tortricidae). *Ann. ent. Soc. Queb.* 6:59-69.
- Peck, O. 1951. Superfamily Chalcidoidea. In C.F.W. Muesebeck, K. V. Krombein, and H.K. Townes, Hymenoptera of America North of Mexico, Synoptic Catalogue pp. 410-494. U. S. Dept. Agr. Monogr. 2, 1420 pp.
- Peck, O. 1963. A catalogue of the nearctic Chalcidoidea (Insecta: Hymenoptera). *Can. Ent. Supplement* 30:1092 pp.
- Reinhard, H. J. 1955. North American tachinid flies of the genus *Wagneria* (Diptera). *J. Kans. ent. Soc.* 28:49-59.
- Sabrosky, C. W. and P. H. Arnaud. 1965. Family Tachinidae. In A. Stone, C. W. Sabrosky, W. W. Wirth, R. H. Foote, J. R. Coulson. A catalogue of the Diptera of America north of Mexico. U. S. Dept. Agric. Handbook No. 276, 1696 pp.
- Sanjean, J. 1957. Taxonomic studies of *Sarcophaga* larvae of New York, with notes on the adults. *Cornell Exp. Sta. Mem.* 349, 115 pp.
- Schaffner, J. V. and C. L. Griswold. 1934. Macrolepidoptera and their parasites reared from field collections in the northeastern part of the United States. *Misc. Publs U. S. Dept. Agric.* No. 188, 160 pp.
- Short, J. R. T. 1952. The morphology of the head of the larval Hymenoptera with special reference to the head of Ichneumonoidea, including a classification of the final instar larvae of the Braconidae. *Trans. R. ent. Soc. Lond.* 103:27-84.
- Snow, S. J. 1925. Observations on the cutworm, *Euxoa auxiliaris* Grote, and its principal parasites. *J. econ. Ent.* 18:602-609.
- Strickland, E. H. 1916. The army cutworm *Euxoa (Chorizagrotis) auxiliaris* Grote. *Can. Dept. Agric. Ent. Br. Bull.* No. 13. 31 pp.
- Strickland, E. H. 1921. Parasites of the pale western cutworm in Alberta. *Can. Ent.* 53: 97-100.
- Strickland, E. H. 1923. Biological notes on parasites of prairie cutworms. *Can. Dept. Agric. Bull.* 26 (new series). 40 pp.
- Taylor, R. L. 1929. The biology of the white pine weevil, *Pissodes strobi* (Peck), and a study of its insect parasites from an economic viewpoint. *Ent. Am.* 10:1-86.
- Thompson, W. R. 1945. A catalogue of the parasites and predators of insect pests, Section I. Parasite-host catalogue Part 6 Parasites of the Lepidoptera (Cl-f). Commonwealth Institute of Biological Control (Imperial Parasite Service) Belleville, Ontario.
- Tothill, J. D. 1913. Tachinidae and some Canadian hosts. *Can. Ent.* 45:69-75.
- Tothill, J. D. 1924. A revision of the nearctic species of the genus *Gonia* (Diptera, Tachinidae). *Can. Ent.* 56:196-200.
- Townes, H., M. Townes, and V. K. Gupta. 1961. A catalogue and reclassification of the Indo-Australian Ichneumonidae. *Mem. Am. Ent. Inst.* No. 1, 522 pp.
- Treherne, R. C. 1915. A preliminary list of parasitic insects known to occur in Canada. *Rep. ent. Soc. Ont.* 46:178-193.
- Vance, A. M. 1927. On the biology of some ichneumonids of the genus *Paniscus* Schrk. *Ann. ent. Soc. Am.* 20:405-415.

- Viereck, H. L. 1916. The Hymenoptera, or wasp-like insects of Connecticut. Conn. Geological and Natural History Survey Bulletin No. 22, 824 pp.
- Walkden, H. H. 1943. Cutworm and armyworm populations in pasture grasses, wastelands, and forage crops. J. econ. Ent. 36:376-381.
- Walkden, H. H. 1950. Cutworms, armyworms, and related species attacking cereal and forage crops in the central great plains. U. S. Dept. Agric. Cir. 849:1-50.
- Webster, R. L. 1911. Notes on the wheat-head armyworm (*Meliana albilinea* Hubner) as a timothy pest. J. econ. Ent. 4:179-184.
- Whitehouse, F. C. 1922. Ann. Rept. Dept. Agric. Alberta. 1920-1, Edmonton pp. 191-219.
- Wood, G. W. 1951. An annotated list of lepidopterous larvae from commercial blueberry fields, Charlotte County, N. B. Can. Ent. 83:241-244.
- Wood, G. W., and W. T. A. Nielson. 1957. Notes on life-histories of four species of climbing cutworms collected from low-bush blueberry fields in New Brunswick (Lepidoptera: Phalaenidae). Can. Ent. 89:502-506.
- Wood, G. W. and W. T. A. Nielson. 1960. Notes on life-history and parasites of *Syngrapha epigaea* (Grt.) (Lepidoptera: Noctuidae). Can. Ent. 92:759-761.
- Wood, G. W., W. T. A. Neilson, C. W. Maxwell, and J. A. McKiel. 1954. Life-history studies of *Spaelotis clandestina* (Hurr.) and *Polia purpurissata* (Grt.) (Lepidoptera: Phalaenidae) in low-bush blueberry areas in New Brunswick. Can. Ent. 86:169-173.
- Zuska, J. 1963. The puparia of the European species of the family Larvaevoridae (Diptera) I (Subfamily Salmaciinae, Part I). Acta Entomologica Musei Nationalis Prague 35:333-372.